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Seabirds at sea in relation to oceanography

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SEABIRDS AT SEA IN RELATION TO OCEANOGRAPHY

A

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SEABIRDS AT SEA IN RELATION TO OCEANOGRAPHY

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ABSTRACT

This study investigated the macroscale distribution of seabirds in relation to oceanography in a neritic environment characterized by well-defined water masses (the northern Bering Sea) and an oceanic environment characterized by weaker differences between water masses (the northern North Pacific Ocean).

In the northern Bering Sea, the total density (birds/km^2) of all seabirds combined and densities and/or frequencies of occurrence of seven of nine species of seabirds that exhibited significant differences among water masses showed the strongest attraction to Anadyr Water. In general, attractions were second highest in Bering Shelf Water, third highest in Two-layered Water (Alaska Coastal Water overlying Bering Shelf Water), and lowest in Alaska Coastal Water. This pattern of seabird distributions reflected distributions of zooplankton biomass, which were highest in Anadyr Water and consisted of species that were large enough to be eaten directly by seabirds. Further, whereas copepods in Bering Shelf Water also are large, they are much smaller in Alaska Coastal Water and, thus, must pass through more trophic levels to fishes before the energy is directly accessible to seabirds. Consequently, zooplankton-based food webs dominated in Anadyr and Bering Shelf waters and fish-based food webs dominated in Two-layered and Alaska Coastal waters. In addition, seabirds concentrated near a strong, mesoscale thermal front between Bering Shelf and Alaska Coastal waters.

In the northern North Pacific, assemblages of seabirds exhibited three main groupings, a "subarctic assemblage," a "transitional assemblage," and a "subtropical/tropical assemblage." These assemblages matched those for zooplankton, squids, and fishes in the same vicinity, suggesting that there are geographically- and temporally-stable biological communities in the North Pacific that are associated with

well-defined, persistent physical environments. The total density of all seabirds combined and densities and/or frequencies of occurrence of 13 of 16 species of seabirds that exhibited significant two-way ANOVAs exhibited primarily a water mass effect; only one species exhibited primarily a year effect, and two exhibited primarily an interaction (i.e., a change in habitat use between years).

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SALIENT THOUGHTS

. . . No man will be a sailor who has contrivance enough to get himself into a jail; for being in a ship is being in jail with the chance of being drowned. . . . A man in jail has more room, better food, and commonly better company. . . .

--Dr. Samuel Johnson

Studying seabirds at sea is notoriously difficult and it takes a certain kind of character to persist with it. . . . One has a picture in one's mind of a team of hardy little souls, lashed to the masts of groaning and listing ships, stoically counting seabirds coming in and dinners going out. They should really be given an ornithological medal, or at least a permanent job. . . .

--Patricia Monaghan
(*Ibis* 130: 462 [1988])

I tell you, you guys [scientists] have just scratched the surface of that balance-of-nature thing.

--Unidentified very drunk woman (Gladys?)
to Robert Day in the Piptide Bar, Newport,
Oregon, 26 July 1985

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I conducted research on several ships during this study. My first thanks go to Capts. Kiyoshi Masuda and Takeji Fujii of the T/V *Oshoro Maru*, on which I worked in 1982, 1984, 1985, and 1987. I also thank the Bridge Officers (Genji Kobayashi, Gen Anma, Hidekazu Yamaguchi, Toshimi Meguro, Shogo Takagi, and Seiji Sasaki), Radio Operators (Mitsuo Kurotori, Tetsuya Nakamura, the late Hiroaki Ohno, and Satoshi Ishigaki), Purser (Tadamichi Tsugoshi), Engineers (Yasuaki Takii, Ichiro Kataoka, Jun-ichi Kimura, and Fumio Fujimoto), and the crew of the *Oshoro* (especially Bo'suns Kazumi Takano and Haruyoshi Futami; Quartermasters Ryuji Uemoto, Toshihiro Iwamori, and Yoshiharu Matsui; Sailors Toshiharu Yosoe, Noriyasu "Rocky" Takahashi, Yukio Tabata, and Yoshitaka Yoshida; Firemen Ken-ichi Endoh, Shiuichi Hasegawa, and Senetsu Nakai; and Steward Tsutomu Takahashi). You all made me part of your life and work and were the best bunch of mates that I have ever sailed with. I'll never forget you.

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INTRODUCTION

The study of the at-sea distribution of seabirds only recently has entered a phase in which distributions are being interpreted with respect to oceanography. Because ornithologists believed for many years that the ocean was only flat and wet, and because no ornithologists were trained in oceanography until recently, it took a long time for them to understand that there were interpretable patterns of at-sea distributions of seabirds. For many years, the distribution of seabirds was interpreted to consist simply of inshore, offshore, and oceanic or pelagic distributions, depending on the distance from land and the continental shelf (Wynne-Edwards 1935), and little attempt was made to determine how these distributions might be driven by oceanographic characteristics (however, see Jespersen 1930 and Murphy 1936). Later (the 1940s to the mid-1970s), a new phase of study began, in which the basic outlines of at-sea geographic ranges of many species began to be pieced together (e.g., Dixon and Starrett 1952, Gill 1967, King 1974). Still, however, the picture was so fragmentary that a book on marine zoogeography that was written in the 1970s (Briggs 1974) made no mention of zoogeographic or oceanographic patterns of distribution of seabirds. It was not until the mid-late 1970s that researchers began tying the distribution of seabirds to oceanographic characteristics. This research was pioneered by workers such as V. P. Shuntov at TINRO in Vladivostok, USSR (Shuntov 1972), D. G. Ainley and his research group at Point Reyes Bird Observatory (e.g., Ainley and Jacobs 1981, Ainley and Boekelheide 1983, Ainley *et al.* 1986, Fraser and Ainley 1986, Wahl *et al.* 1989), G. L. Hunt, Jr., and his research group at University of California--Irvine (e.g., Hunt *et al.* 1981b, 1990; Hunt and Schneider 1987; Schneider *et al.* 1987, 1990; Harrison 1990; Hunt 1990; Veit and Hunt 1991), K. T. Briggs and his research group at University of California--Santa Cruz (e.g., Briggs

and Chu 1986, Briggs *et al.* 1987), R. Pocklington at the Bedford Institute of Oceanography (Pocklington 1979), and others (e.g., Joiris 1976, Brown 1979, Harrison 1982, Gould 1983, Abrams 1985, Abrams and Underhill 1986).

The at-sea distribution of seabirds may be examined at three primary scales that reflect different scales of oceanographic processes: macroscale (hundreds to thousands of kilometers), mesoscale (tens to hundreds of kilometers), and microscale (meters to kilometers). Each scale, in turn, reflects different levels of habitat selection by seabirds. For example, macroscale distributions may best be thought of as selection of a particular water mass (e.g., subarctic, subtropical, neritic versus oceanic); a terrestrial analog might be whether a bird species selects for a forest, a grassland, or a rocky mountain top. Mesoscale distributions may best be thought of as selection of intermediate-scale variations in habitats within water masses or at the boundary between water masses (e.g., fronts, upwelling areas); a terrestrial analog might be whether a forest-nesting bird species nests and feeds in a coniferous forest or a deciduous forest. Microscale distributions may best be thought of as habitat selection at a local scale and as selection that reflects responses to fine-scale variations in habitats (e.g., microscale convergences or divergences at the ocean's surface, presence of sea ice, presence of *Sargassum* in tropical waters); a terrestrial analog might be whether a species nesting and feeding in a coniferous forest forages at the ends of branches, near the trunk of the tree, or near the top of the tree (e.g., see MacArthur 1958).

A hidden assumption of the research to date on relationships between seabirds and oceanographic characteristics is that the scale of sampling for seabirds is appropriate to the scale at which the oceanographic processes occur, and, hence, that it reflects the distribution of seabirds with respect to those processes (Wiens 1985, Schneider and Piatt 1986). As Briggs *et al.* (1987) have observed, seabirds resemble terrestrial birds in that

their distributions best fit environmental characteristics when examined from a macroscale aspect. Studies of responses of seabirds to mesoscale processes are only now being conducted (e.g., Haney and McGillivary 1985a,b), and it is unclear when, if ever, reasonable relationships between seabirds and microscale processes can be deduced. Hence, the study of macroscale distributions is the best place to begin learning about the relationships between seabirds and oceanographic characteristics.

While conducting research and traveling at sea in the 1970s and early 1980s, I began to realize that many aspects of the macroscale distribution of birds at sea appeared to be interpretable in terms of oceanography. Further, it became apparent to me that the ocean was not simply flat and wet to seabirds, but that they instead responded to it as if it was an area with hills and valleys, forests and hedgerows, and deserts and marshes. I therefore decided to investigate some of the ways in which seabirds at sea responded to oceanography. The objective of this study was to investigate some aspects of the macro- and mesoscale distribution of seabirds in relation to oceanography. The overall null hypothesis was that the at-sea distribution of seabirds does not reflect macro- and mesoscale oceanographic characteristics. To achieve this objective, I studied the at-sea distribution of seabirds in a neritic environment that was characterized by well-defined water masses and a well-defined mesoscale front (the northern Bering Sea) and in an oceanic environment that was characterized by weaker differences between large water masses (the northern North Pacific Ocean). I examined both types of environment because, even had I found interpretable patterns of seabird distribution in the neritic environment, I was unsure that I would find interpretable patterns in the oceanic parts of the northern North Pacific. I also examined interannual stability of patterns of seabirds and their environment in the northern North Pacific Ocean.

NORTHERN BERING SEA

Recent work in the northern Bering Sea indicates that there are several discrete water masses, each with different origins (Coachman *et al.* 1975, Grebmeier 1987, Springer 1988, Walsh *et al.* 1989). These water masses lie side by side, yet differ in rates of primary production by as much as a factor of six. In addition, patterns of nutrient availability differ among these water masses, with mid-summer concentrations of nitrates differing by factors of 25 or more.

Patterns of food web transfer of energy also differ among the water masses. The westernmost water mass (Anadyr Water), which incorporates water from the continental slope of the central Bering Sea, contains a high biomass of large oceanic copepods and a diversity of fish species. The central water mass (Bering Shelf Water), which incorporates zooplankton and food webs from the southern Bering Sea shelf, contains medium-sized shelf copepods that occur in moderate biomass. In contrast, the eastern water mass (Alaska Coastal Water) incorporates a coastal food web containing small, nearshore copepods and is dominated by fishes.

These differences in food webs are thought to play an important role in structuring the nesting distribution of seabirds in the northern Bering Sea. For example, differences in the distribution and biomass of certain types of copepods are thought to restrict the distribution of colonies of Least Auklets in this area to locations near the oceanic water mass or the shelf water mass (Springer and Roseneau 1985). Further, the high productivity of the oceanic system also allows a diversity of fishes that then are available to piscivorous seabirds. In contrast to the large zooplankton in the oceanic water mass (i.e., Anadyr Water), the small size of zooplankters in the coastal water mass is believed to result in a food web at the top of which is a seabird assemblage dominated by piscivorous species (Springer *et al.* 1987).

The NSF-funded research program ISHTAR (Inner SHelf Transfer And Recycling) was organized to study some of these patterns of differing productivity among the water masses of the northern Bering and southern Chukchi seas, including differences in species-assemblages of phytoplankton and zooplankton, nutrient recycling, and nutrient and energy pathways. I investigated some of the ways in which these biological differences in water masses affect the organization of seabird communities at sea and, specifically, the ways in which these differences caused differences in the at-sea distribution and densities of seabirds in the northern Bering Sea. (In this study, the term "density" refers to numbers of birds/km^2 and the term "sigma-t" refers to [oceanographic] density of the water-column.) I hypothesized that: (1) the differences in water masses (documented by the ISHTAR studies) would lead to differences in distributions and densities of seabirds; (2) most species would be more abundant in Anadyr Water than in Alaska Coastal Water, because of differences between these two water masses in patterns of production and in food webs; (3) the intermediate amount of energy available to upper trophic levels in Bering Shelf Water would yield seabird densities intermediate between those of the other two main water masses; and (4) an oceanographic front separating Bering Shelf Water from Alaska Coastal Water would form an important feeding area for seabirds. To test these hypotheses, I studied the at-sea, quantitative distribution of seabirds in the northern Bering Sea in September 1985.

Background

The shelf of the northern Bering Sea may be divided into three water masses having different origins and characteristics (Fig. 1; Coachman 1986). These water masses are called (from west to east): Anadyr Water, Bering Shelf Water, and Alaska Coastal Water. The ISHTAR research group defines these water masses primarily by

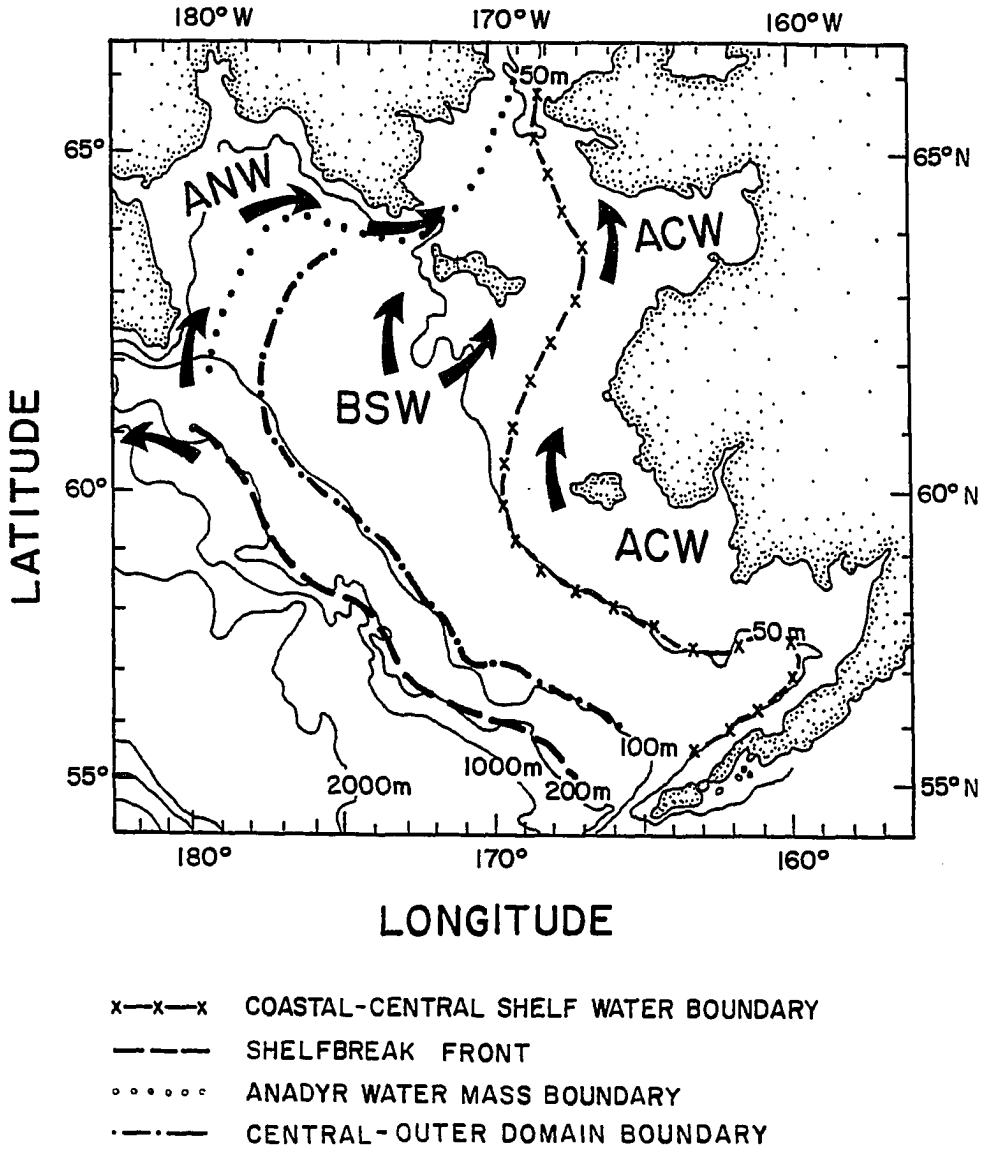

Figure 1. Approximate locations of major fronts, water masses, and current flow on the Bering Sea shelf (modified from Coachman 1986 and Hansell *et al.* 1989). Abbreviations for water masses are: ANW = Anadyr Water; BSW = Bering Shelf Water; ACW = Alaska Coastal Water.

salinity, with Anadyr Water having salinities ≥ 32.4‰, Bering Shelf Water having salinities 31.5-32.4‰, and Alaska Coastal Water having salinities < 31.5‰ (also see Coachman and Shigaev, in press).

Anadyr Water originates on the continental slope of the western Bering Sea. There, the northwestward-flowing Bering Slope Current bifurcates near Cape Navarin, USSR, into the northward-flowing Anadyr Current and the southward-flowing East Kamchatka Current (Fig. 1; also see Kinder *et al.* 1975). The Anadyr Current brings cool, high-salinity and high-nutrient water northward into Anadyr Gulf. From there, this water flows eastward, then mainly northward, primarily through Anadyr Strait between Cape Chukotskiy, USSR, and St. Lawrence Island, USA. Additional, minor flow around the southern and eastern coasts of St. Lawrence Island also occurs in some years and during some months (Walsh *et al.* 1989). Anadyr Water moves northward primarily in the western Chirikov Basin and eventually exits the Bering Sea through the western side of Bering Strait (Fig. 1; also see Kinder *et al.* 1986).

Modified Bering Shelf Water is a mixture of Bering Shelf Water and upper-layer Outer Shelf Water (Iverson *et al.* 1979) of the southeastern and central Bering Sea. The former water mass is represented by the Middle Domain, and the latter water mass lies at the surface of the Outer Domain (Iverson *et al.* 1979). These two water masses are separated by the strong Middle Front in the southeastern Bering; this front extends northwestward into the eastern edge of Anadyr Gulf, where it apparently ends (Fig. 1; also see Walsh *et al.* 1989). At this northern location, Outer Shelf Water escapes around the end of the front and mixes with the widespread Bering Shelf Water, forming modified Bering Shelf Water (hereafter called Bering Shelf Water). This modified water then moves northward through both Anadyr and Shpanberg straits (Fig. 1) and is characterized by moderate salinities and extremely low (< 0°C) bottom temperatures.

North of St. Lawrence Island, Bering Shelf Water covers most of the central and eastern Chirikov Basin and exits the basin primarily on the eastern side of Bering Strait (Coachman *et al.* 1975).

Alaska Coastal Water is a northerly extension of the Coastal Domain (Iverson *et al.* 1979, Coachman 1986) of the southeastern Bering Sea. In the northern Bering, it is modified by additional warm, fresh water added primarily by the Yukon and Kuskokwim rivers. Alaska Coastal Water occurs in the extreme eastern part of the northern Bering Sea, including Norton Sound, and exits the region at the surface through eastern Bering Strait (Fig. 1). It is warm and of low salinity, so it often overrides adjacent Bering Shelf Water at the surface just south of Bering Strait (Coachman *et al.* 1975).

Nutrients vary among water masses, with the most nutrients found in Anadyr Water at all times of the year (as much as 25 μM NO_3^-). Because this water originates in the Bering Sea Basin and transgresses much of the shelf as a bottom current, essentially no nutrients are lost to primary production until the water shoals onto the shallow northern Bering shelf (Hansell *et al.* 1989, Hansell and Goering 1990). Concentrations of nutrients in Bering Shelf Water are less than those in Anadyr Water. Alaska Coastal Water, in contrast, exhibits very low concentrations of nutrients (usually < 1 μM NO_3^-) after the initial spring bloom.

These water masses also exhibit differences in patterns of primary production (Springer 1988, Hansell *et al.* 1989, Walsh *et al.* 1989). Alaska Coastal Water exhibits the traditional, "textbook" pattern of a spring bloom, with all of the nutrients eventually becoming tied up in phytoplankton biomass, because of a time lag in the production and growth of grazing zooplankton. The rate of primary production drops dramatically in this low-nutrient water after the spring bloom in April and May; annual primary production is thought to be on the order of 50 g C/m^2/yr (Walsh *et al.* 1989). In contrast, Anadyr

Water provides a continual and concentrated supply of nutrients from the deeper part of the Bering Sea. Production is considerably higher and more protracted in this water mass (approximately 285 g C/m^2/yr; Walsh *et al.* 1989), although not as high as was proposed earlier (Sambrotto *et al.* 1984). Apparently, stability of the water column must occur and must be maintained for a period long enough to allow enhanced productivity. This phenomenon occurs primarily in the Chirikov Basin and north of Bering Strait, with the "west" bloom occurring roughly in a north-south band in the Chirikov Basin (Hansell *et al.* 1989, Walsh *et al.* 1989). In addition to the high production of phytoplankton north of St. Lawrence Island and north of Bering Strait, the constant inflow of water from off the shelf advects large quantities of phytoplankton into the area (Hansell *et al.* 1989, Walsh *et al.* 1989). Stability and advection apparently are also important in production in Bering Shelf Water; the "east" bloom also is stable in space and time, occurring in a north-south band from the eastern end of St. Lawrence Island to Bering Strait. In addition, large quantities of phytoplankton are advected into this area from farther south (approximately 0.8 x 10^8 g chlorophyll/day; Hansell *et al.* 1989).

Zooplankton concentrations and species-composition also vary among the water masses (Springer *et al.* 1989, Walsh *et al.* 1989). The oceanic copepods *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* dominate in Anadyr Water and constitute 70-90% of the zooplankton biomass in the western part of the northern Bering Sea. These zooplankters average approximately 5 g/m^2 (dry weight) during mid-summer, with densities apparently consistent from year to year. The smaller *Calanus marshallae* is the dominant copepod in Bering Shelf Water, accounting for 70-90% of the calanoid biomass and averaging approximately 0.2-1.0 g/m^2 (dry weight) during summer, with significant annual variations in abundance. Alaska Coastal Water is dominated by small, nearshore copepods such as *Pseudocalanus* spp., *Eurytemora* spp.,

and *Acartia longiremis*. Data on biomass in this water mass are few, but these small zooplankters appear to average approximately 1.0-1.5 g/m^2 (dry weight) during summer.

Food webs reflect these differences in origins of the water masses and production by phytoplankton. Anadyr Water contains large quantities of the large grazing oceanic copepods, although primary production still greatly exceeds grazing rates overall (Springer *et al.* 1989, Walsh *et al.* 1989). Some of this excess production enters benthic food webs, and some is advected north out of the area (Grebmeier 1987, Grebmeier *et al.* 1988; Coachman and Shigaev, in press). The constant advection of these large oceanic copepods into the area allows the presence of a well-developed pelagic food web and large colonies of both planktivorous and piscivorous seabirds (Springer 1988, Springer *et al.* 1989). Some of the phytoplankton production in Bering Shelf Water falls out of suspension, supporting well-developed benthic systems (Grebmeier 1987, Grebmeier *et al.* 1988, Walsh *et al.* 1989). In Bering Shelf Water, the presence of the medium-sized *C. marshallae* also allows a moderately-developed pelagic food web. Alaska Coastal Water supports much lower primary production, with more steps in the food web being required to produce food large enough to be eaten by apex predators such as birds. Consequently, the amount of carbon consumed by seabirds in Alaska Coastal Water is approximately one-fourth that consumed by seabirds in Anadyr Water (Walsh *et al.* 1989), and seabird colonies in Alaska Coastal Water are small and scattered (Sowls *et al.* 1978, Springer *et al.* 1987).

NORTHERN NORTH PACIFIC OCEAN

The oceanic, northern North Pacific Ocean provides a good setting for examining macroscale relationships between seabirds and the marine environment. First, it is a large basin, one of the largest in the world. Second, the basin is deep, with most of the water

between Alaska and Hawaii 4000-5000+ m deep; hence, bathymetric fluctuations do not cause pronounced variation in oceanographic characteristics, as has been seen in studies over the continental shelf (e.g., Briggs *et al.* 1987). There also are major seabird colony complexes at the northern and southern limits of this large expanse of open water: on the Hawaiian Islands and in southern and western Alaska. A large complement of non-breeding seabirds also "winters" there during the boreal summer; hence, requirements of most species to remain at least in the vicinity of breeding colonies are relaxed, allowing most species to feed in what may be "better" (i.e., optimal) locations for maximizing energy gain.

This study examined several aspects of the relationships between seabirds and oceanographic characteristics in the northern North Pacific Ocean, between Alaska (55°00'N) and Hawaii (21°20'N), during the summer of 1984 and along the same station line between 55°00'N and 36°30'N during the summer of 1985. The first question was whether there were oceanographic habitats (i.e., water masses) that could be described in an objective way with known physical oceanography of the region. The second question was whether the distributions of the seabirds reflected the locations and characteristics of these habitats and whether those relationships could be linked to biological and physical characteristics of the habitats. The third question was whether those relationships were stable over time. High stability in relationships over time would suggest that habitat specialization is occurring or has occurred, whereas low stability would suggest that oceanographic dynamics are so variable as to obscure repeatable patterns, that random patterns of foraging (rather than habitat specialization) are resulting in non-repeatable patterns, or that variables are measured on inappropriate scales. Specifically, the objectives of this study were to describe interannual patterns of physical structure of the oceanic, northern North Pacific in 1984 and 1985, to describe interannual patterns of

densities of zooplankton, fishes, and squids there in 1984 and 1985 as indicators of biological productivity and prey availability, to describe the patterns of at-sea distribution of seabirds there in both years, and to explain how these distributions were related to the oceanographic structure of this area.

Background

The oceanic, northern North Pacific Ocean may be divided into four major water masses and two major fronts that will be considered in this study to be water masses. North of the Subarctic Front is Subarctic Water and its southerly component, the Transition Domain (Dodimead *et al.* 1963, Favorite *et al.* 1976). South of the Subtropical Front is Subtropical Water (sometimes called North Pacific Central Water). Between these two great oceanic fronts lies the Transition Zone, in which the water gradually changes in character from subarctic to subtropical (Roden 1970, 1971, 1972, 1977, 1980). [Note that the Transition Zone of Roden (1970, 1971, 1972, 1977, 1980) is different from the Transition Domain of Dodimead *et al.* (1963) and Favorite *et al.* (1976). The latter is the southernmost domain of the subarctic water mass, which lies north of the Subarctic Front (see above); in contrast, the former lies to the south of the Subarctic Front. The position of the Transition Zone is determined in the North Pacific primarily by the convergence of Ekman transports (Roden 1970).]

Primary and secondary productivity in the subarctic waters are unusual, in that a bloom is seen in secondary, rather than primary, production (Heinrich 1962). Phytoplankton in the subarctic North Pacific do not exhibit a bloom because, unlike the pattern seen in other oceanic systems, some zooplankton there (*Neocalanus cristatus* and *N. plumchrus*) reproduce at depth during winter and produce young that are in surface waters as the spring increase in primary production begins (Heinrich 1962, Miller *et al.*

1984). Consequently, the standing stock of phytoplankton is grazed early and remains constant, whereas the standing stock of zooplankton (these two species and *Eucalanus bungii*) increases during the summer (Heinrich 1962, Cooney and Coyle 1982, Miller *et al.* 1984, Cooney 1987). These three species may represent up to 75% of the zooplankton biomass in the upper 2,000 m of the subarctic North Pacific (Miller *et al.* 1984).

In contrast to the pattern seen for the subarctic North Pacific, standing stocks of both phytoplankton and zooplankton in the lower-latitude Subtropical Water are extremely low, perhaps 10-20% of those seen in subpolar gyres (Blackburn 1981). The zooplankters also are smaller than are those seen in subarctic waters (Blackburn 1981). In addition, there is a lag between bursts of primary production and production of young that can help graze the production; standing stocks of phytoplankton remain relatively low all year, however, because they are nutrient limited (Blackburn 1981).

Zooplankton in the northern North Pacific fall into three main assemblages (Fager and McGowan 1963). The subarctic assemblage is dominated by three euphausiids (*Euphausia pacifica*, *Thysanoessa longipes*, and *Tessarabrachion oculatus*), a chaetognath (*Sagitta elegans*), and a pteropod (*Limacina helicina*). The transitional assemblage is dominated by three euphausiids (*Euphausia gibboides*, *Nematoscelis difficilis*, and *Thysanoessa gregaria*). The subtropical assemblage is dominated by nine species of euphausiids, four species of chaetognaths, and six species of pteropods that range over most of the equatorial and subtropical waters of the Pacific.

METHODS

DATA COLLECTION

General

Seabird transect data were collected on a series of strip-transects that are 10 min of time while the ship was moving ahead in a straight line at a uniform speed; this is the primary sampling method used for counting seabirds at sea (Gould *et al.* 1982, Tasker *et al.* 1984, Gould and Forsell 1989). Transects were 300 m wide and, multiplied by the distance traveled in 10 min, were approximately 1 km^2 in area at typical speeds (approximately 11 kt). During each transect, the following data were collected: coordinates, ship's speed (to the nearest 0.1 kt), and numbers of seabirds of each species. For each transect, the total number of seabirds of all species combined and numbers of seabirds of each species were divided by the area sampled, to calculate the total density of all species combined and densities of seabirds of each species, respectively. These are relative densities rather than absolute densities, but they are treated as absolute densities in all analyses (see Gould *et al.* 1982, Tasker *et al.* 1984, and Gould and Forsell 1989).

Northern Bering Sea

Data were collected during the period 14-22 September 1985. CTD data were collected at 88 stations. Six station lines crossed the boundary between Bering Shelf Water and Alaska Coastal Water (with two Bering Strait lines overlying the same location but being sampled on successive days), and three station lines crossed the boundary between Anadyr Water and Bering Shelf Water (Fig. 2; also see Fig. 5). Seabird data

were collected with the above methods at 272 seabird transect "stations" during the same period (Fig. 2).

Northern North Pacific Ocean

Data were collected along 155°00'W longitude in the northern North Pacific Ocean from 16 July to 4 August 1984 and from 3 to 18 July 1985. The 1984 cruise of the *Oshoro Maru* sampled between 55°00'N 155°00'W (south of Kodiak Island, Alaska) and approximately 25°00'N 155°00'W, and then to 21°20'N 157°32'W, off the southeastern corner of Oahu Island, Hawaii. The 1985 cruise of the *Oshoro Maru* sampled between 55°00'N 155°00'W and 36°30'N 155°00'W in the northern North Pacific.

Oceanographic, zooplankton, and fisheries data were collected at a series of stations along station lines during both cruises. CTD, zooplankton, and fisheries data were published in the *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 (1985) and 29 (1986) for the years 1984 and 1985, respectively. This data compilation is published annually by the Faculty of Fisheries, Hokkaido University, Hakodate, Japan.

CTD data were collected at 36 stations in 1984 (30 between 55°00'N and 36°30'N and the remainder between there and 25°00'N) and 31 stations in 1985 (all between 55°00'N and 36°30'N). Sea-surface temperature and salinity data were collected with a Tsurumo Seiki continuously-recording thermosalinograph attached to the sea chest; the water intake was 3-4 m below the water's surface.

Zooplankton samples were collected in the upper 150 m of the water column with a NORPAC net fitted with a flow-meter and a net of 0.350 mm mesh. Samples were preserved in formalin and later were analyzed as wet-weight biomass (g/1000 m^3) of zooplankton at each station. Some samples were heavily contaminated with

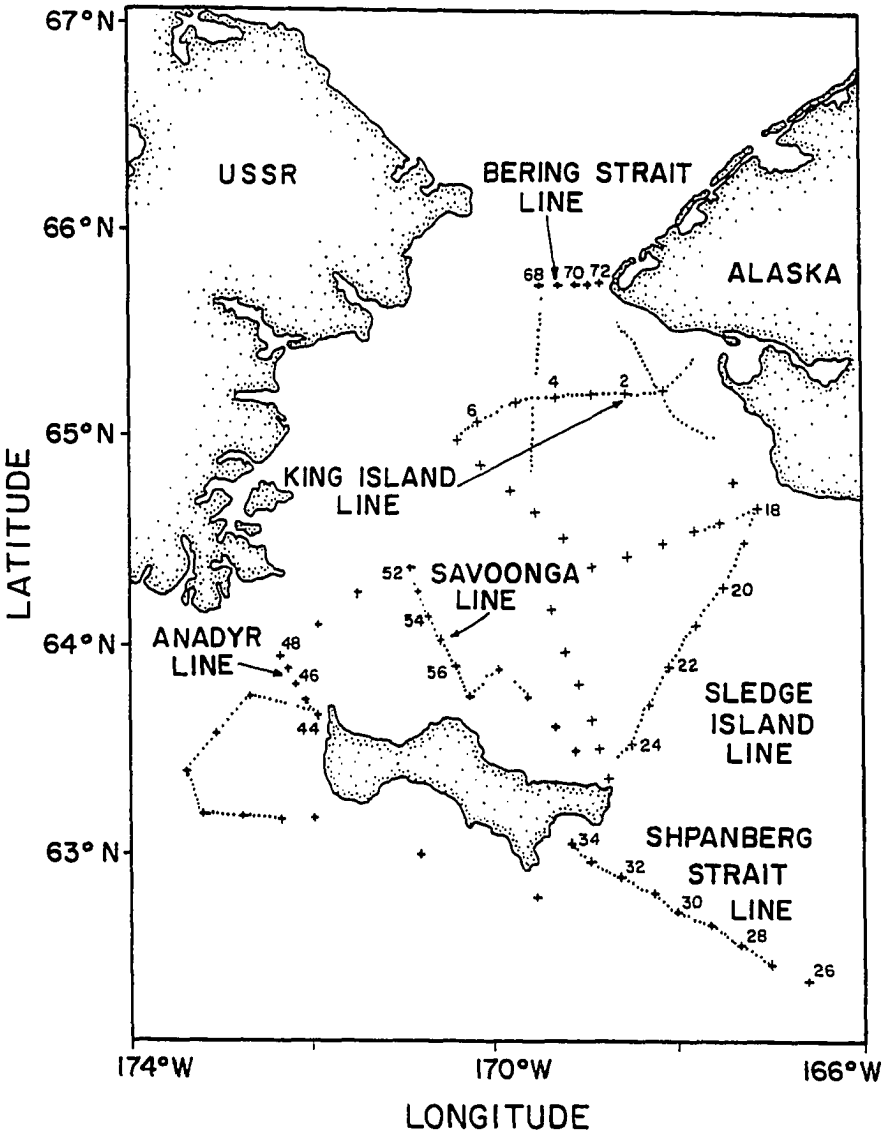

Figure 2. Locations of hydrographic stations (crosses, some with accompanying station numbers) and seabird transect stations (small dots), 14-22 September 1985, with selected station lines referred to in text.

phytoplankton or salps; data from these stations were not included in the analyses of zooplankton biomass. Data were collected at 36 stations in 1984 (30 between 55°00'N and 36°30'N and the remainder between there and 25°00'N) and 31 stations in 1985 (all between 55°00'N and 36°30'N).

Fisheries data were collected at 16 drift gill-net test-fishing stations between 55°00'N and 36°30'N during both 1984 and 1985. The gill-nets were of similar length each year (129-132 units of net in 1984 and 131-132 units in 1985, with a length of approximately 50 m/unit) and were fished each evening from approximately 1 h before local sunset (usually 19:00-20:00 local time) to approximately first light (usually 04:00-05:00 local time). These nets fished for a diversity of fishes and squids. Stretched mesh-sizes ranged from 29 mm to 204 mm, but most units were in the sizes 115-130 mm, which are the primary sizes for catching salmon and neon flying squid. All fisheries data were standardized as CPUEs of each species (number caught/unit of net fished) for each fishing station.

Seabird data were collected with the above methods on 620 transects in 1984 and 456 transects in 1985. Complete coverage of the transect line was attempted during both years, but data were not collected in the areas 52°00'-51°30'N, 34°40'-32°30'N, 31°00'-29°00'N, 26°50'-24°55'N, and 23°15'-21°55'N in 1984 and in all areas south of 36°30'N in 1985.

DATA ANALYSIS

General

Before analyses, the data were stratified into water masses that were defined by physical characteristics described in the literature and by CTD data collected in 1984 and

1985. Water-column structure and geographic extents of water masses were determined by plotting temperature, salinity, and sigma-t data from the oceanographic stations.

For the biomass of zooplankton, CPUEs of fishes and squids, the total density of all seabird species combined, and densities of each seabird species, Kruskal-Wallis tests evaluated the null hypotheses that biomass, CPUEs, and densities did not differ among water masses. When a test revealed significant differences in densities among water masses, nonparametric multiple comparisons tests (Conover 1980: 230-233) were used to determine which water masses were significantly different.

To indicate the sizes of densities in the different water masses, I calculated means and standard errors of total density and of densities of each seabird species. Because data on seabird densities usually are not normally distributed, information on medians would be more appropriate. Essentially all medians were zero, however, because of the often-patchy nature of the distribution of seabirds at sea.

Because some species appeared to have occurred in such low densities that I could not detect differences in densities among water masses, I also tested for differences in frequencies of occurrence (i.e., numbers of transects on which birds occurred/water mass) among water masses. I tabulated the data on frequencies of occurrence of all birds combined and of selected seabird species in each water mass and tested for differences in frequencies with Chi-square (χ^2) contingency tables for row (presence/absence) x column (water mass) independence (Conover 1980, Zar 1984). The null hypothesis for such tests was that frequencies did not differ among water masses. When significant differences were found, individual cells (i.e., water masses) were examined for large contributions to the χ^2 values. Significance levels for all statistical tests were $\alpha = 0.05$.

Northern Bering Sea

I tested the water masses for differences in seabird densities with Kruskal-Wallis tests, as described above. Following ISHTAR conventions, criteria for separating the water masses in 1985 were: Anadyr Water--$\geq$ 32.4‰; Bering Shelf Water--31.5-32.4‰; and Alaska Coastal Water--< 31.5‰ (Coachman 1987; C. P. McRoy, University of Alaska, Fairbanks, AK, pers. comm.). In addition to the water masses described previously, I classified a new "water mass" (Two-layered Water) that consisted of Bering Shelf Water on the bottom and Alaska Coastal Water at the surface, but I am unsure of the temporal stability of this water mass. Thus, the seabird transect data were stratified by four oceanographic strata or "habitats": Anadyr Water anywhere in the water column, Bering Shelf Water throughout the water column, Two-layered Water, and Alaska Coastal Water throughout the water column. As described above, I also calculated means and standard errors of seabird densities and used χ^2 tests to evaluate whether frequencies of occurrence differed among the four water masses.

To determine relationships between water masses and primary prey types and primary feeding methods, I used published information (e.g., Ashmole 1971, Hunt *et al.* 1981a, Springer *et al.* 1984) to classify the seabirds as primarily zooplankton feeders versus fish/nekton feeders and primarily diving feeders versus surface feeders. Because some species are omnivorous (e.g., Northern Fulmar, gulls), I was unable to categorize them into primary prey types. The combined density data then were tested for differences among the four water masses with Kruskal-Wallis tests, as described above.

To determine whether the front between Bering Shelf Water and Alaska Coastal Water was important to seabirds, I plotted the data on seabird densities for the Shpanberg Strait, Sledge Island, and King Island station lines (see Fig. 2) and determined the distances (in km) from the centers of the thermal fronts. For each station line, I then

tested for changes in densities from the fronts with Spearman rank correlations (Zar 1984). At each station line, the tests evaluated the hypothesis for all species combined and for each selected species that densities did not change with distance from the front(s). I then tested the null hypotheses that the number of significant tests occurred in a frequency that one would expect to occur randomly (χ^2 goodness-of-fit test; Zar 1984) and that the probability of getting a positive and a negative slope for a test was equal (binomial test; Zar 1984).

Northern North Pacific Ocean

I tested for differences in zooplankton biomass and CPUEs of fishes and squids between water masses with a two-way ANOVA (Zar 1984) with untransformed data for both years, south to 36°30'N. The two-way ANOVA tests for a year effect, a water mass effect, and a water mass-year interaction. If water mass effects were found, multiple comparisons from Kruskal-Wallis tests for each year were used to determine which water masses were significantly different. An interaction was interpreted as being important only if it was significant at the same or a higher level than were the main effects and it made statistical sense (see below); otherwise, the main effects were interpreted as being important.

I tested for differences in densities of seabirds among water masses with Kruskal-Wallis tests with multiple comparisons and with two-way ANOVAs, as described above. In the results section, results of multiple comparisons are presented first. Because two additional water masses were sampled in 1984, the results of the two-way ANOVAs are presented separately. Two-way ANOVAs were used with the 1984 data south to 33°00'N (i.e., including all of the Transition Zone Water) and the 1985 data south to 36°30'N (i.e., within the same water mass) to test for a year effect, a

water mass effect, and a water mass-year interaction; interactions and main effects were examined as above. Prior to analysis, the data were transformed with a logarithmic transformation, which helps to normalize positively-skewed distributions (Zar 1984: 239). As described above, I also calculated means and standard errors of seabird densities and used χ^2 contingency tables for row (presence/absence) x column (water mass) independence to evaluate whether frequencies of occurrence differed among the four water masses.

RESULTS

NORTHERN BERING SEA

Distribution of water masses

CTD sections for the Shpanberg Strait Line indicated the presence of two primary water masses: Bering Shelf Water and Alaska Coastal Water (Fig. 3a). The thermal section indicated a core of cold Bering Shelf Water on the bottom between Stations 33 and 30. Warm water east of Station 29 apparently was Alaska Coastal Water, with strong thermal fronts between Stations 31 and 29 and between Stations 34 and 33, near the coast of St. Lawrence Island. The dividing line between the two water masses was just west of Station 29, as indicated by the location of the 31.5‰ isohaline on the salinity section. No salinity front occurred on this station line, and Alaska Coastal Water only slightly overrode Bering Shelf Water at the surface, resulting in a very narrow band of Two-layered Water. The sigma-t section indicated a lack of resistance to vertical motion at the same locations as those indicated by the thermal fronts.

The Sledge Island Line also indicated the presence of two primary water masses: Bering Shelf Water and Alaska Coastal Water (Fig. 3b). There was a double thermal front, with what appeared to be either upwelling in the center and warmer Alaska Coastal Water to the east of Station 21, or a cold core on the bottom of the frontal zone that may have been a cold bottom remnant of Bering Shelf Water from farther south. The 31.5‰ isohaline intersected the surface at or near Station 21. Northeast of this station, a strong salinity front occurred to just southwest of Station 19. Lower-salinity water occurred immediately northeast of Station 19, near the southern coast of the Seward Peninsula; I assume that this low-salinity water represents some of the input from the Yukon River. Apparently, Alaska Coastal Water overrode the Bering Shelf Water slightly, with the

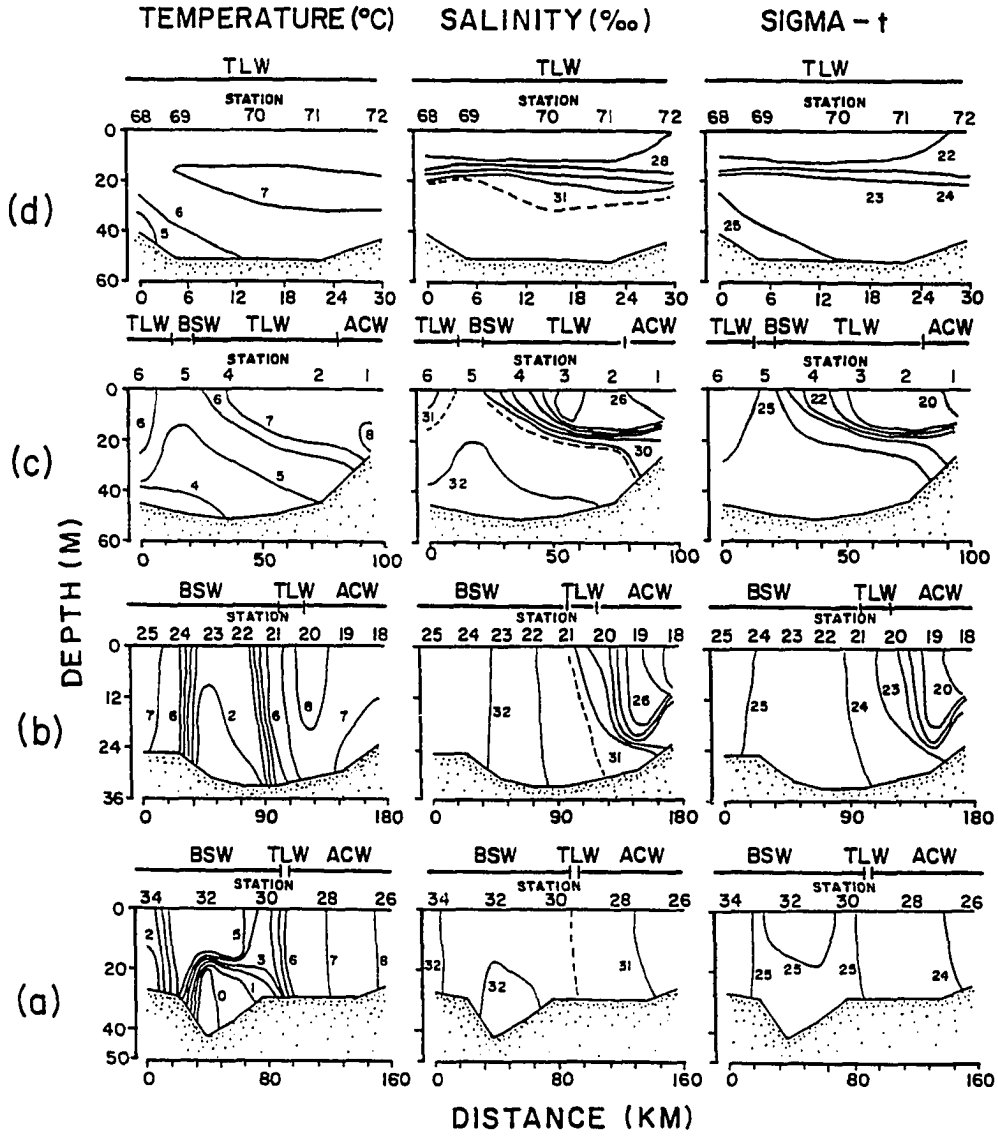

Figure 3. Vertical sections of temperature, salinity, and sigma-t on the (a) Shpanberg Strait, (b) Sledge Island, (c) King Island, and (d) Bering Strait lines, 15-21 September 1985. (Data were provided by C. P. McRoy of the ISHTAR project.) On the salinity section, the dashed line indicates the boundary (31.5‰) between Bering Shelf Water and Alaska Coastal Water. Abbreviations for water masses are: BSW = Bering Shelf Water; TLW = Two-layered Water; ACW = Alaska Coastal Water.

overlap occurring as a band of Two-layered Water between Stations 21 and 20. There was a strong sigma-t front around Stations 20-19, at the same location as the salinity front, and there was resistance to vertical motion throughout this line.

There were two water masses on the King Island Line: Bering Shelf Water and Alaska Coastal Water (Fig. 3c). There was a thermal front between Stations 6 and 4, with what appeared to be upwelling in the center of this front (as indicated by both the thermal and the sigma-t plots). The salinity structure was similar, with Alaska Coastal Water in the surface layer east of Station 5 (as indicated by the 31.5‰ isohaline) and with Alaska Coastal Water significantly overriding Bering Shelf Water (i.e., with Two-layered Water) at the surface. At the surface west of the midpoint between Stations 6 and 5 was low-salinity water that may have been a remnant of the larger Alaska Coastal Water mass overlying the Bering Shelf Water. A strong salinity front occurred between Stations 5 and 3, with lower-salinity water found east of Station 3. The sigma-t section followed the pattern seen for the salinity section, with the water column vertically stratified and a lack of resistance to vertical motion around Station 5.

The Bering Strait Line was highly stratified, with what appeared to be Alaska Coastal Water overlying Bering Shelf Water (Fig. 3d). No thermal or salinity fronts were present. Data for a second Bering Strait Line (not shown here but collected the following day) were similar to those for the line shown in Figure 3d, with Alaska Coastal Water overlying Bering Shelf Water and with no thermal or salinity fronts present. The sigma-t section followed the pattern seen for the salinity section, with the water column vertically stratified and resistance to vertical motion throughout this line.

Anadyr Water and Bering Shelf Water were present in a broad area from southwest to northwest of St. Lawrence Island (Figs. 4a and 4b). Anadyr Water occurred west of Station 38 southwest of St. Lawrence Island (not shown), east to

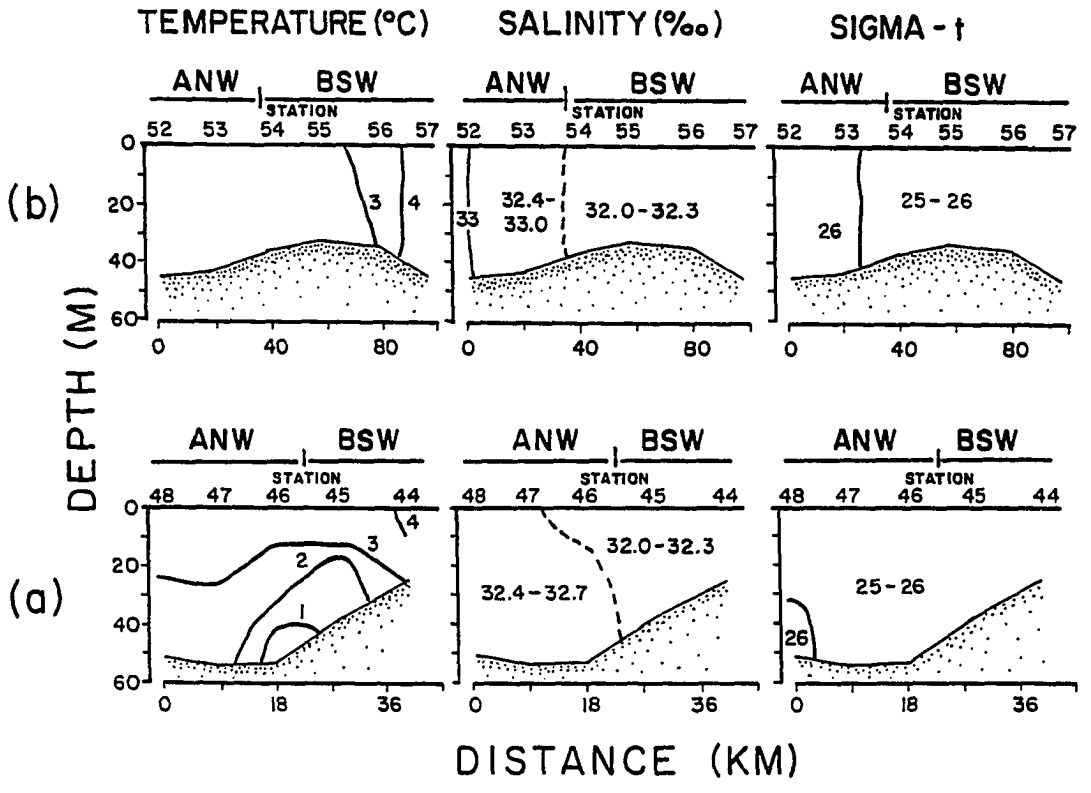

Figure 4. Vertical sections of temperature, salinity, and sigma-t on the (a) Anadyr and (b) Savoonga lines, 18-19 September 1985. (Data were provided by C. P. McRoy of the ISHTAR project.) On the salinity section, the dashed line indicates the boundary (32.4‰) between Anadyr Water and Bering Shelf Water. Abbreviations for water masses are: ANW = Anadyr Water; BSW = Bering Shelf Water.

between Stations 46 and 45 at depth on the Anadyr Line (Fig. 4a), and east to near Station 54 on the Savoonga Line (Fig. 4b), as indicated by the presence of water ≥ 32.4‰ west of this line; all other water on these lines was < 32.4‰ (i.e., Bering Shelf Water). The thermal section indicated a pool of cold Anadyr Water on the bottom of the Anadyr Line (Fig. 4a), and the sigma-t section indicated that there was resistance to vertical motion on both lines.

Thus, three main water masses and a two-layered system were sampled during this cruise: Anadyr Water in the area west of St. Lawrence Island, Bering Shelf Water throughout the central and southern parts of the study area, and Alaska Coastal Water throughout the eastern part of the study area (Fig. 5). In addition, because surface layers of Alaska Coastal Water overrode Bering Shelf Water in the northern part of the study area, there was a discrepancy between surface and bottom waters in the location of the boundary between these two main water masses (Fig. 5); this multi-layered area was classified as Two-layered Water.

Distribution of seabirds in water masses

Twenty-nine species of seabirds were recorded at the 272 seabird transect stations: loons (Red-throated, Pacific, and Common), tubenoses (Northern Fulmar, Short-tailed Shearwater), a cormorant (Pelagic), sea ducks (Common, King, and Steller's eiders; Oldsquaw; White-winged Scoter), phalaropes (Red-necked and Red), jaegers (Pomarine, Parasitic, and Long-tailed), gulls (Herring, Glaucous-winged, and Glaucous gulls; Black-legged Kittiwake), and alcids (Common and Thick-billed murres; Pigeon Guillemot; Ancient Murrelet; Parakeet, Least, and Crested auklets; Tufted and Horned puffins). Eight species were found in highly nearshore waters or were only migrating through the area (loons, sea ducks), and seven other species were so rare that I clearly

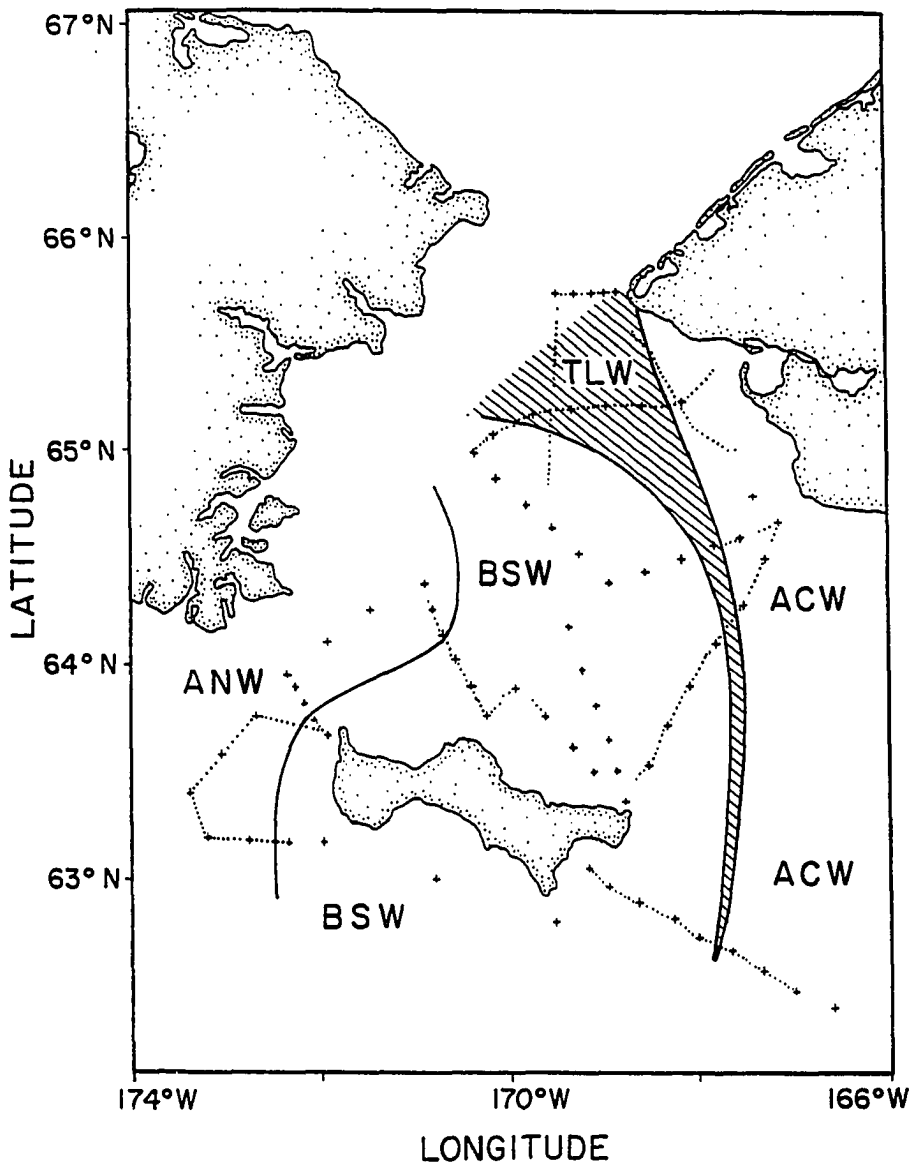

Figure 5. Approximate geographical extent of water masses in the study area, 14-22 September 1985, as determined from CTD data. Abbreviations for water masses are: ANW = Anadyr Water; BSW = Bering Shelf Water; TLW = Two-layered Water; ACW = Alaska Coastal Water.

was unable to do any quantitative analyses on them. I conducted further analyses on the remaining 14 species and on the total density of all species combined.

Total densities of all species combined differed significantly among the four water masses, with Anadyr Water > Bering Shelf Water = Two-layered Water > Alaska Coastal Water (Table 1). The maximal density on a transect was approximately 506 birds/km^2 in Anadyr Strait; high densities were seen in the Anadyr Strait area in general and in Anadyr Water (and sometimes Bering Shelf Water) north of St. Lawrence Island. Total frequencies of occurrence of seabirds per transect also differed among water masses: birds occurred on essentially all transects in all water masses except Alaska Coastal Water, where they occurred only about 83% of the time (Table 2).

Densities of Northern Fulmars differed significantly among the four water masses, with Anadyr Water > Bering Shelf Water = Two-layered Water = Alaska Coastal Water (Table 1). A similar pattern was seen in the frequency data, in that this species occurred most frequently in Anadyr Water, less frequently in Bering Shelf Water and Two-layered Water, and not at all in Alaska Coastal Water (Table 2). The maximal density was approximately 10 birds/km^2 in southern Anadyr Strait; high densities occurred in the Anadyr Strait area in general.

Densities of Short-tailed Shearwaters differed significantly among the four water masses, with Anadyr Water = Bering Shelf Water = Two-layered Water > Alaska Coastal Water (Table 1). A similar pattern occurred in the frequency data: this species occurred most frequently in Anadyr Water and Bering Shelf Water, less frequently in Two-layered Water, and was essentially absent from Alaska Coastal Water (Table 2). Main areas of concentration were north of St. Lawrence Island, where densities of up to 455 birds/km^2 were recorded, in Anadyr Strait, and along the front between Bering Shelf Water and Alaska Coastal Water (see below).

Table 1. Densities (birds/km^2) of seabirds in four water masses in the northern Bering Sea, Alaska, 14-22 September 1985.

	Water mass								
	Anadyr Water (n = 39)		Bering Shelf Water (n = 106)		Two-layered Water (n = 62)		Alaska Coastal Water (n = 65)		Kruskal-Wallis H
Total density/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 3)[1]
TOTAL DENSITY	66.2	16.6	32.5	6.8	12.2	2.2	5.5	1.9	91.973*
Northern Fulmar	1.6	0.3	0.3	< 0.1	0.2	0.1	0	-	91.466*
Short-tailed Shearwater	30.4	14.3	4.9	1.1	1.2	0.4	< 0.1	< 0.1	53.767*
Red Phalarope	1.1	0.3	1.0	0.4	0.3	0.1	0.9	0.4	9.727*†
Pomarine Jaeger	0.4	0.1	0.3	0.1	0.2	0.1	0	-	17.030*†
Glaucous Gull	0.1	0.1	0.1	< 0.1	0.2	0.1	0.2	0.1	4.797
Black-legged Kittiwake	2.4	0.8	1.2	0.2	3.5	1.2	0.9	0.2	14.573*†
Common Murre	3.8	1.4	1.0	0.2	0.6	0.1	< 0.1	< 0.1	55.354*
Thick-billed Murre	0.3	0.1	0.1	< 0.1	< 0.1	< 0.1	0	-	21.553*†
Ancient Murrelet	0	-	0.3	0.1	0.9	0.4	0.1	0.1	7.272
Parakeet Auklet	< 0.1	< 0.1	0.1	< 0.1	0.4	0.2	0.1	< 0.1	7.325
Least Auklet	16.5	6.2	19.5	6.3	0.3	0.1	0.1	0.1	89.374*
Crested Auklet	7.7	1.7	1.5	0.4	0.8	0.3	0.1	< 0.1	61.521*
Tufted Puffin	0.1	< 0.1	0.4	0.2	1.1	0.3	< 0.1	< 0.1	21.386*†
Horned Puffin	0.2	0.1	0.2	< 0.1	0.4	0.1	0.1	< 0.1	7.543*†

[1] * = significant at $\alpha = 0.05$; † = multiple comparisons revealed no significant pairwise differences in densities.

Table 2. Frequencies of occurrence (No.) and percent occurrences (%) of seabirds in four water masses in the northern Bering Sea, Alaska, 14-22 September 1985.

	Water mass								
	Anadyr Water (n = 39)		Bering Shelf Water (n = 106)		Two-layered Water (n = 62)		Alaska Coastal Water (n = 65)		χ^2
Total frequency/species	No.	(%)	No.	(%)	No.	(%)	No.	(%)	(df = 3)[1]
TOTAL FREQUENCY	39	(100.0)	103	(97.2)	61	(98.4)	54	(83.1)	21.657*
Northern Fulmar	30	(76.9)	22	(20.8)	9	(14.5)	0	(0)	88.351*
Short-tailed Shearwater	22	(56.4)	55	(51.9)	16	(25.8)	2	(3.1)	52.728*
Red Phalarope	12	(30.8)	17	(16.0)	6	(9.7)	12	(18.5)	7.738
Pomarine Jaeger	10	(25.6)	20	(18.9)	9	(14.5)	0	(0)	16.661*
Glaucous Gull	4	(10.3)	6	(5.7)	8	(12.9)	9	(13.8)	3.796
Black-legged Kittiwake	25	(64.1)	55	(51.9)	40	(64.5)	27	(41.5)	8.378*
Common Murre	26	(66.7)	41	(38.7)	19	(30.6)	1	(1.5)	34.454*
Thick-billed Murre	8	(20.5)	5	(4.7)	2	(3.2)	0	(0)	20.737*§
Ancient Murrelet	0	(0)	10	(9.4)	7	(11.3)	2	(3.1)	7.197
Parakeet Auklet	1	(2.6)	4	(3.8)	9	(14.5)	6	(9.2)	8.429*
Least Auklet	25	(64.1)	67	(63.2)	9	(14.5)	2	(3.1)	88.791*
Crested Auklet	29	(74.4)	39	(36.8)	16	(25.8)	5	(7.7)	31.220*
Tufted Puffin	3	(7.7)	15	(14.2)	18	(29.0)	2	(3.1)	19.247*
Horned Puffin	4	(10.3)	12	(11.3)	11	(17.7)	2	(3.1)	7.234

[1] * = significant at $\alpha = 0.05$. § = possible inflation of the χ^2 value to significance from expected value(s) <5.

Densities of Red Phalaropes appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise comparisons (Table 1). The frequency data also indicated that there were no significant preferences for water masses (Table 2). The maximal density was approximately 30 birds/km^2 near the front between Bering Shelf Water and Alaska Coastal Water (see below).

Densities of Pomarine Jaegers appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise differences in densities (Table 1). In contrast, the frequency data indicated that this species occurred most frequently in Anadyr Water, less frequently in Bering Shelf Water and Two-layered Water, and not at all in Alaska Coastal Water (Table 2). Although densities were not high anywhere (the maximum was approximately 7 birds/km^2 in Bering Strait), my impression was that these birds concentrated in areas where large numbers of other seabirds aggregated. These birds are kleptoparasitic, feeding at sea primarily by stealing food from other seabirds (Ashmole 1971).

Densities of Glaucous Gulls did not differ significantly among the four water masses (Table 1). Mean densities were consistently low throughout all habitats, with a maximal density of only 3 birds/km^2 near Bering Strait. A similar pattern occurred in the frequency data, in that this species exhibited no consistent patterns of attraction to or avoidance of water masses. Because this species was seen on only 27 of 272 transects (Table 2), densities were too low overall to allow detection of real differences in habitat use.

Densities of Black-legged Kittiwakes appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise differences (Table 1). In contrast, the frequency data indicated a preference for Anadyr Water and Two-layered Water (Table 2). This species occurred commonly in all water masses,

however, and was the only species seen at more than 50% of the seabird transect stations. The maximal density was approximately 71 birds/km^2 near Bering Strait.

Densities of Common Murres differed significantly among the four water masses, with Anadyr Water > Bering Shelf Water = Two-layered Water > Alaska Coastal Water (Table 1). Similarly, this species occurred most frequently in Anadyr Water, less frequently in Bering Shelf Water and Two-layered Water, and essentially not at all in Alaska Coastal Water (Table 2). The maximal density was approximately 54 birds/km^2 in the vicinity of Anadyr Water southwest of St. Lawrence Island; high densities in general were seen in Anadyr Strait.

Densities of Thick-billed Murres appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise differences (Table 1), probably because this species was seen on only 15 of 272 transects. The frequency data indicated a strong preference for Anadyr Water, with this species rarely present in Bering Shelf Water and Two-layered Water and entirely absent from Alaska Coastal Water (Table 2). Because almost 90% of the χ^2 test statistic came from cells with expected values < 5, the total value may have been inflated thereby to a significant level (see Zar 1984). Thus, there almost certainly was a preference for Anadyr Water (most records were from Anadyr Strait, with a maximal density of 3 birds/km^2), but densities were too low overall to allow confirmation of real differences in habitat use.

Densities of Ancient Murrelets did not differ significantly among the four water masses (Table 1). Most birds were seen in Bering Strait and in the vicinity of the front between Bering Shelf Water and Alaska Coastal Water; none were seen in Anadyr Water. The frequency data also indicated that there were no significant preferences for water masses. Because birds were seen on only 27 of 272 transects (Table 2), densities of this species were too low overall to allow detection of real differences in habitat use.

Densities of Parakeet Auklets did not differ significantly among the four water masses (Table 1). This species was seen at only 20 of 272 stations, and mean densities were very low throughout the area. In contrast, the frequency data indicated a significant preference for Two-layered Water and Alaska Coastal Water (Table 2). The maximal density was approximately 7 birds/km^2 near the front between Bering Shelf Water and Alaska Coastal Water, east of St. Lawrence Island (see below).

Densities of Least Auklets differed significantly among the four water masses, with Anadyr Water = Bering Shelf Water > Two-layered Water = Alaska Coastal Water (Table 1). A similar pattern occurred in the frequency data, which indicated that this species occurred frequently in Anadyr Water and Bering Shelf Water, infrequently in Two-layered Water, and essentially not at all in Alaska Coastal Water (Table 2). The maximal density was approximately 465 birds/km^2 in Anadyr Water north of St. Lawrence Island; in general, densities were highest in the Anadyr Strait area and north of St. Lawrence Island.

Densities of Crested Auklets differed significantly among the four water masses, with Anadyr Water > Bering Shelf Water = Two-layered Water = Alaska Coastal Water (Table 1). Similarly, this species occurred most frequently in Anadyr Water, less frequently in Bering Shelf Water and Two-layered Water, and rarely in Alaska Coastal Water (Table 2). The maximal density was approximately 44 birds/km^2 in Anadyr Strait; in general, densities were highest there and near the front between Bering Shelf Water and Alaska Coastal Water (see below).

Densities of Tufted Puffins appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise differences (Table 1). In contrast, the frequency data indicated a preference for Two-layered Water (Table 2). The maximal density was 16 birds/km^2 near the King Island Line.

Densities of Horned Puffins appeared to differ significantly among the four water masses, but multiple comparisons revealed no significant pairwise differences (Table 1). Mean densities were uniformly low throughout the area, with the maximal density approximately 6 birds/km^2 near the King Island Line. The frequency data also indicated that there were no significant preferences for water masses (Table 2). Because birds were seen on only 29 of 272 transects, densities of this species were too low overall to allow detection of real differences in habitat use.

Feeding methods, prey types, and water masses

Stratification of the bird data into plankton feeders and fish/nekton feeders showed several clear relationships to water masses (Table 3). Plankton feeders were most abundant in Anadyr Water and Bering Shelf Water, with lower densities in Two-layered Water and Alaska Coastal Water. Fish/nekton feeders exhibited high and similar densities in Anadyr Water, Bering Shelf Water, and Two-layered Water and had lower densities in Alaska Coastal Water. Altogether, 86% of the birds in Anadyr Water and 87% of the birds in Bering Shelf Water were plankton feeders, whereas only 38% of the birds in Two-layered Water and 54% of the birds in Alaska Coastal Water were.

Stratification of the bird data into diving feeders and surface feeders also showed several clear relationships to water masses (Table 3). Diving feeders were most abundant in Anadyr Water and Bering Shelf Water, with densities lower in Two-layered Water and lowest in Alaska Coastal Water. Surface feeders exhibited a different pattern, with densities highest in Anadyr Water and Two-layered Water and lowest in Alaska Coastal Water; densities in Bering Shelf Water were intermediate between these two groups (Table 3). Altogether, 92% of the birds in Anadyr Water, 91% of the birds in Bering

Table 3. Densities (birds/km^2) of prey types and feeding methods of seabirds in four water masses in the northern Bering Sea, Alaska, 14-22 September 1985.

	Water mass								
	Anadyr Water (n = 39)		Bering Shelf Water (n = 106)		Two-layered Water (n = 62)		Alaska Coastal Water (n = 65)		Kruskal-Wallis H
Prey type/feeding method	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 3)[1]
PRIMARY PREY TYPE									
Plankton feeders	55.4	15.8	27.4	6.7	3.9	0.8	1.3	0.4	106.124*
Fish/nekton feeders	8.7	2.3	3.6	0.5	6.3	1.5	1.1	0.2	47.011*
PRIMARY FEEDING METHOD									
Diving feeders	60.4	16.4	28.1	6.6	6.1	0.9	0.6	0.2	130.580*
Surface feeders	5.6	0.9	2.9	0.5	4.4	1.2	2.0	0.5	32.431*

[1] * = significant at $\alpha = 0.05$.

Shelf Water, 58% of the birds in Two-layered Water, and 23% of the birds in Alaska Coastal Water were diving feeders.

Oceanographic fronts and seabird distribution

I examined the correlation of seabird densities with mesoscale oceanographic factors by determining the relationship between the density of seabirds and the distance from the center of the front(s) along the boundary between Bering Shelf Water and Alaska Coastal Water. As seen in Figs. 6, 8, and 10, this boundary consists of one or more strongly-defined thermal fronts.

There were two thermal fronts along the Shpanberg Strait Line: a large one approximately 25 km wide near the center of the station line and a secondary one approximately 5 km wide near the eastern end of St. Lawrence Island (Fig. 6). I chose Station 30 as the center of the main front and a point equidistant between Stations 34 and 33 as the center of the secondary front. Both the total density and the densities of four species of zooplankton feeders exhibited positive association with these thermal fronts (Figs. 6 and 7, Table 4). In contrast, a comparison of the plot for total density with those for the salinity and sigma-t sections in Fig. 3a indicates that there was a poor relationship.

There was one broad thermal frontal zone along the Sledge Island Line. This frontal zone was nearly 80 km wide (Fig. 8), and, because of its extreme width, I divided it into two main frontal regions, each showing rapid horizontal changes in temperature. The westernmost front was centered between Stations 24 and 23, and the easternmost one was centered between Stations 22 and 21 (Fig. 8). Both the total density and densities of five species exhibited positive association with these thermal fronts (Figs. 8 and 9). In contrast, comparison of the plot for total density with those for the salinity and sigma-t sections in Fig. 3b again indicates that there was a poor relationship.

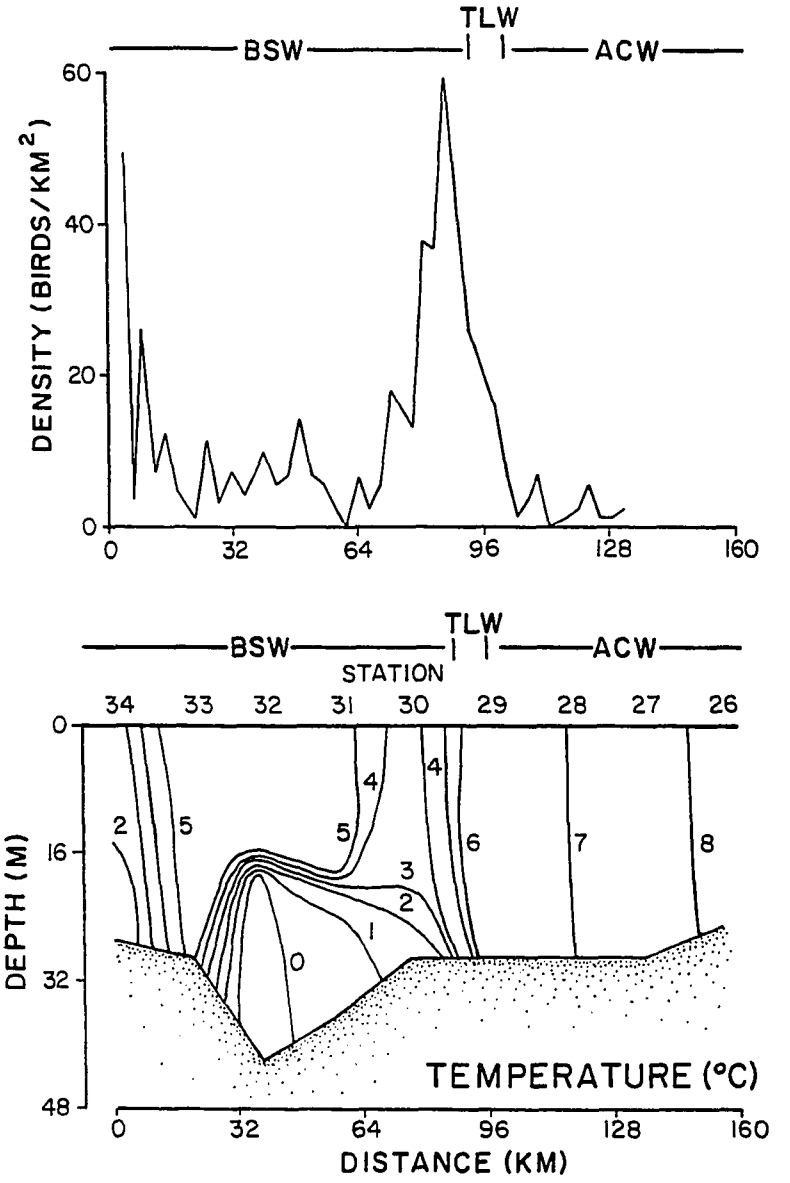

Figure 6. Variations in the total density of seabirds (top) on the Shpanberg Strait Line with respect to thermal structure (bottom), 17 September 1985. Abbreviations for water masses are: BSW = Bering Shelf Water; TLW = Two-layered Water; ACW = Alaska Coastal Water.

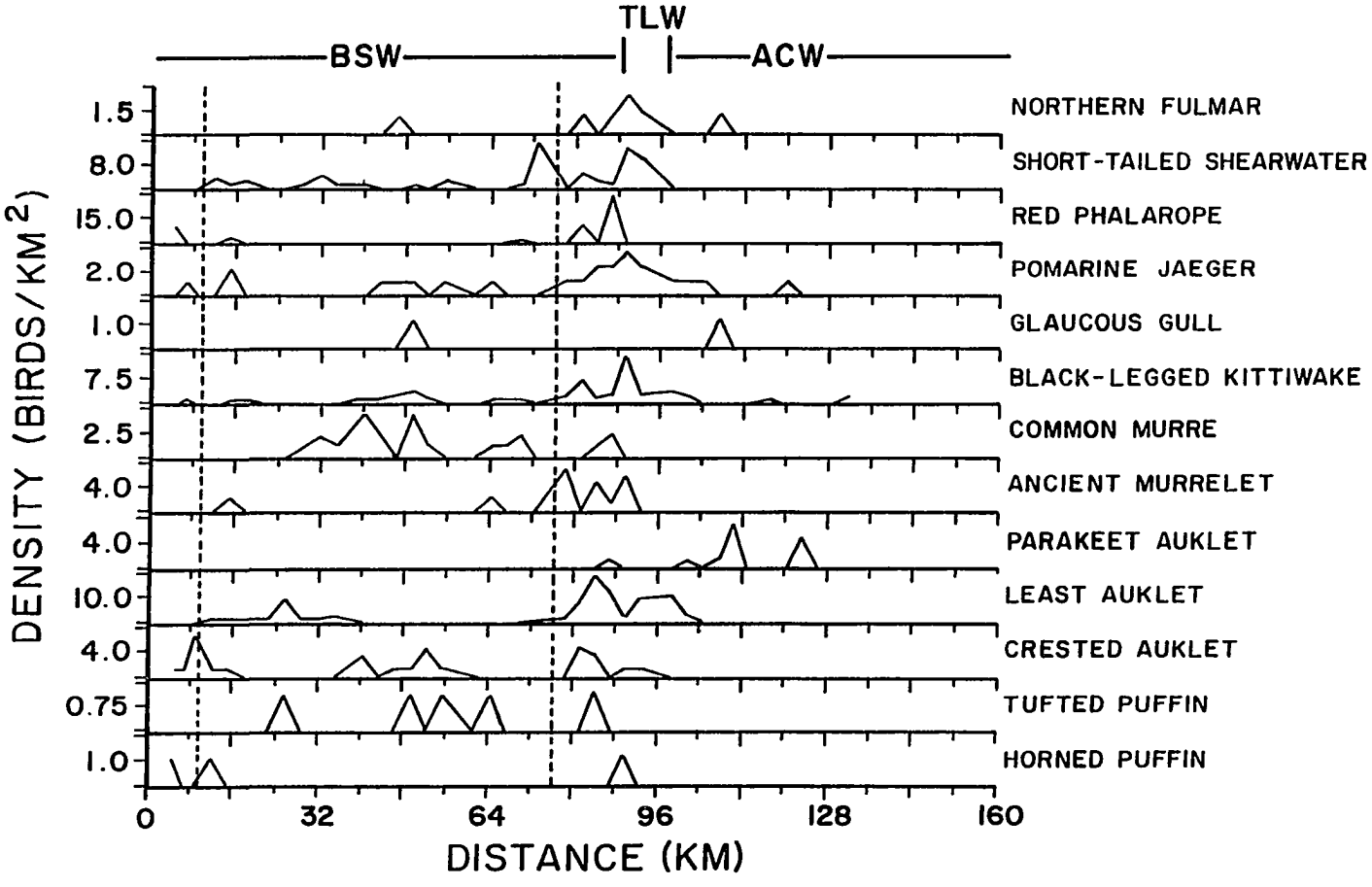

Figure 7. Variations in densities of seabirds on the Shpanberg Strait Line, 17 September 1985. Dashed lines indicate the approximate centers of thermal fronts. Abbreviations for water masses are as in Figure 6.

Table 4. Results of Spearman rank correlations between density of seabirds and distance from the center of the thermal front(s) on three station lines in the northern Bering Sea, Alaska, 14-22 September 1985. Station lines are shown in Figure 2.

Total density/species	Station line: Shpanberg Strait (n = 40)[1]	Sledge Island (n = 42)[1]	King Island (n = 27)[1]
TOTAL DENSITY	-0.497*	-0.647*	-0.765*
Northern Fulmar	-0.040	-0.298*	-0.011
Short-tailed Shearwater	-0.409*	-	-0.641*
Red Phalarope	-0.271	0.207	-0.034
Pomarine Jaeger	-0.178	-0.174	-0.227
Glaucous Gull	-0.109	-0.339*	-
Black-legged Kittiwake	-0.144	-0.054	-0.524*
Common Murre	-0.024	-0.449*	-0.373*
Ancient Murrelet	-0.355*	-0.321*	-
Parakeet Auklet	0.262	0.020	0.169
Least Auklet	-0.336*	-0.484*	0.111
Crested Auklet	-0.356*	0.061	-0.144
Tufted Puffin	-0.080	-	-0.632*
Horned Puffin	-0.287	-	-0.345

[1] * = significant at $\alpha = 0.05$.

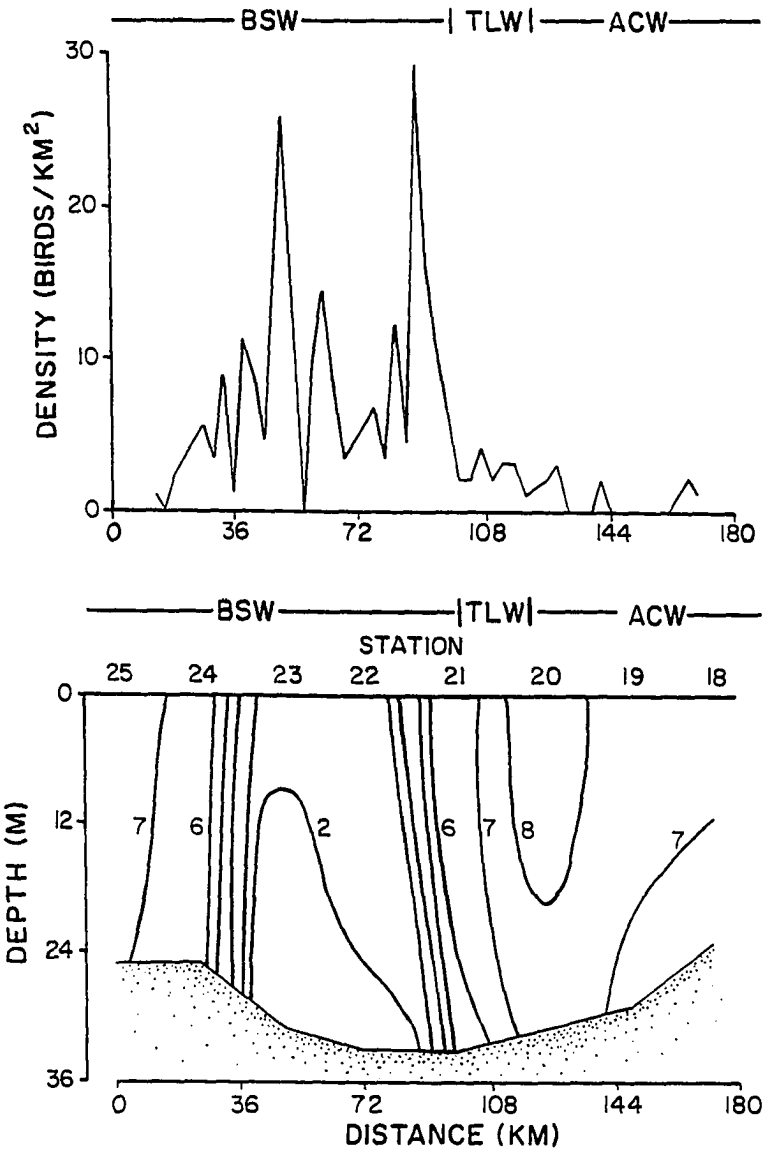

Figure 8. Variations in the total density of seabirds (top) on the Sledge Island Line with respect to thermal structure (bottom), 16 September 1985. Abbreviations for water masses are: BSW = Bering Shelf Water; TLW = Two-layered Water; ACW = Alaska Coastal Water.

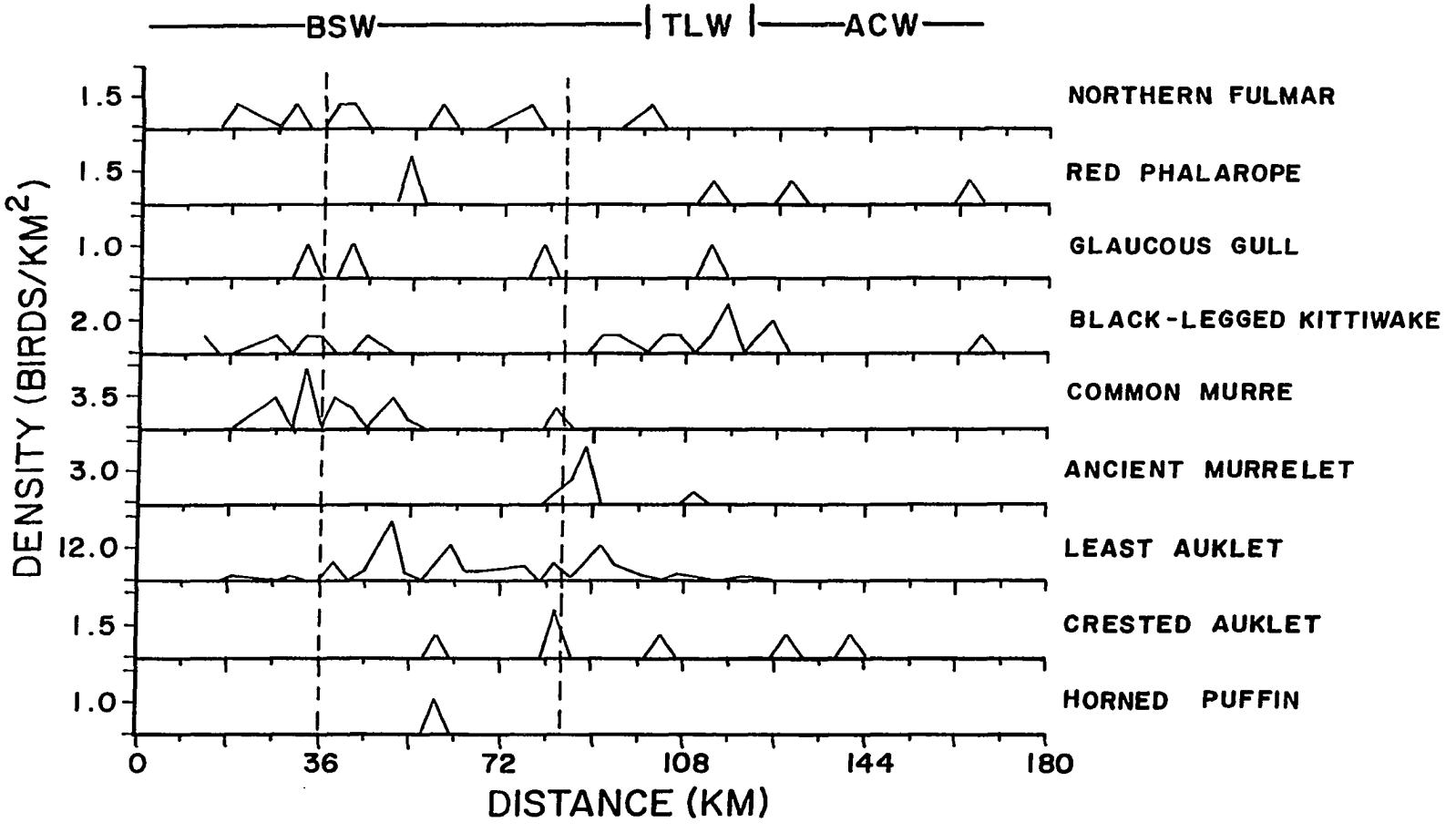

Figure 9. Variations in densities of seabirds on the Sledge Island Line, 16 September 1985. Dashed lines indicate the approximate centers of thermal fronts. Abbreviations for water masses are as in Figure 8.

There was one narrow thermal front along the King Island Line; this frontal zone was less than 30 km wide (Fig. 10). As mentioned previously, I suspected that Anadyr Water occurred just west of this station line. Because of the narrow width of this front, I chose Station 5 as its approximate center. Both the total density and densities of four species (Short-tailed Shearwaters and three species of fish/nekton feeders) exhibited positive association with the thermal front (Figs. 10 and 11). The close correspondence between temperature, salinity, and sigma-t structures in Fig. 3c made it impossible to contrast differing effects of these variables on total densities of birds.

Of the 16 cases showing significant, negative correlations with distance from the fronts, three were of total density (i.e., in all three cases examined), seven were of plankton feeders, four were of fish/nekton feeders, and two were of omnivores (Table 4). Of the seven cases involving plankton feeders, the correlations were significant in both cases involving Short-tailed Shearwaters, both cases involving Ancient Murrelets, two of three cases involving Least Auklets, and one of three cases involving Crested Auklets. The only plankton feeder not exhibiting a consistent association with the fronts was the Parakeet Auklet, which occurred in higher densities away from the fronts, primarily in Alaska Coastal Water. Of the four cases involving fish/nekton feeders, the correlations were significant in one of three cases involving Black-legged Kittiwakes, two of three cases involving Common Murres, and one of two cases involving Tufted Puffins (Table 4). Two cases involved two omnivorous species (Northern Fulmars and Glaucous Gulls; Table 4).

I then examined the question of whether this number of significant tests was abnormal with a χ^2 goodness-of-fit test. Given the large number of tests, one might expect ($0.05 \times 37 =$) ~ 2 of the 37 tests to be significant, just randomly. The 16 significant tests were significantly different from random ($\chi^2 = 103.600$; df = 1; P = 0),

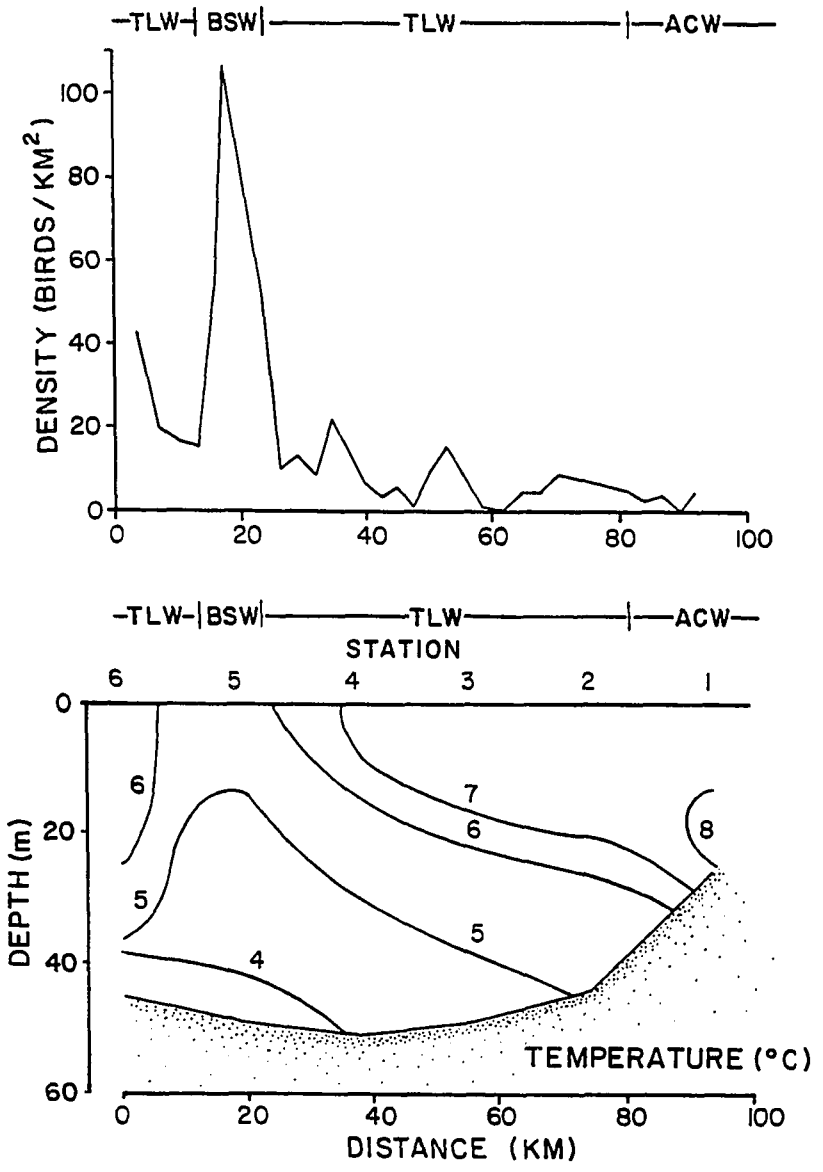

Figure 10. Variations in the total density of seabirds (top) on the King Island Line with respect to thermal structure (bottom), 15 September 1985. Abbreviations for water masses are: TLW = Two-layered Water; BSW = Bering Shelf Water; ACW = Alaska Coastal Water.

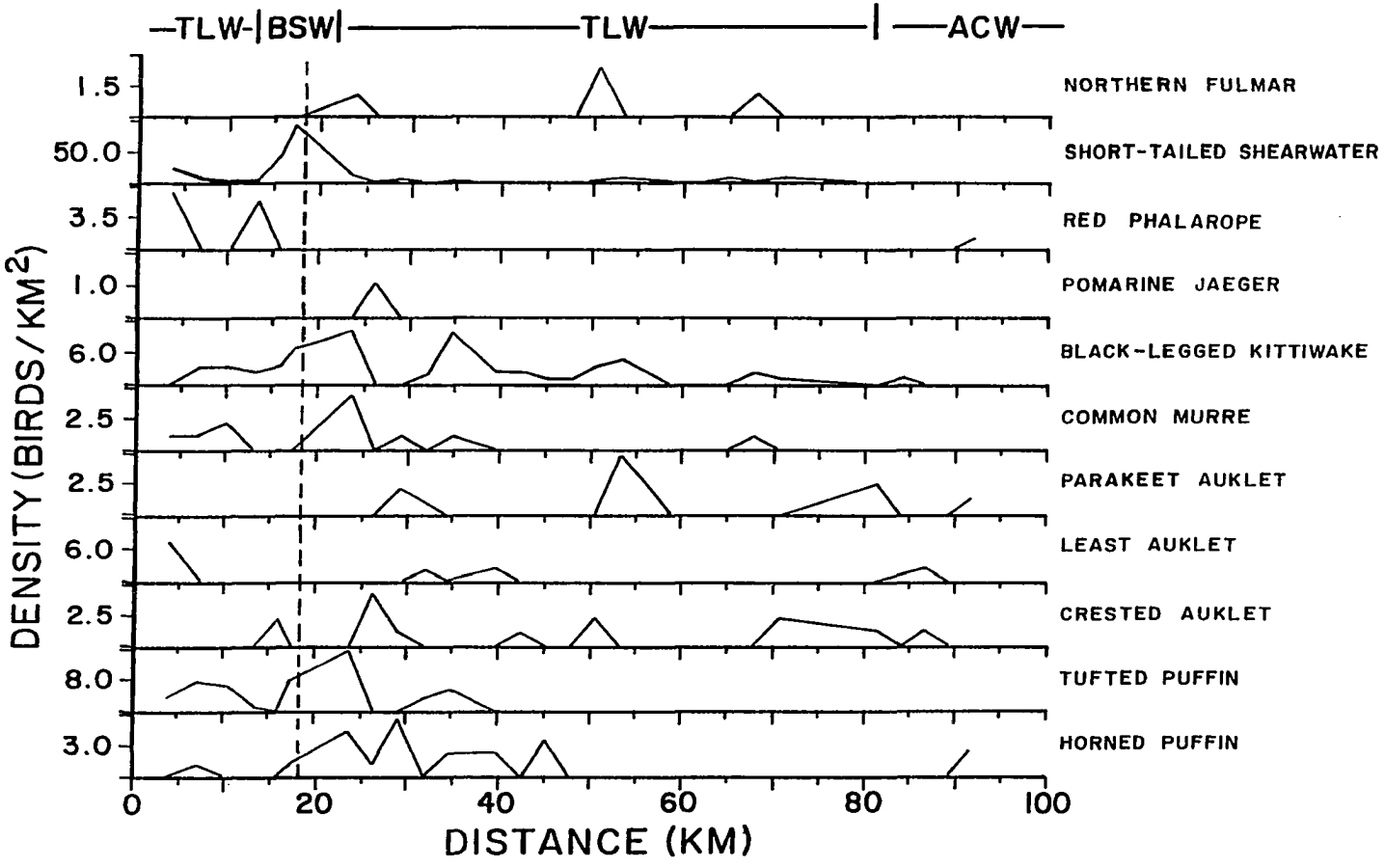

Figure 11. Variations in densities of seabirds on the King Island Line, 15 September 1985. Dashed line indicates the approximate center of the thermal front. Abbreviations for water masses are as in Figure 10.

however, indicating that more results indicated a significant response to fronts than would be expected to occur with $\alpha = 0.05$.

I then examined whether the probability of getting a positive response to increasing distance from oceanographic fronts is the same as getting a negative one (i.e., $P = Q = 0.50$; binomial test). With 6 positive responses and 31 negative responses to increasing distance, significantly more results indicated a negative response to distance than would be expected to occur if the probabilities were equal ($Z = 3.048$; $P = 0.0022$).

NORTHERN NORTH PACIFIC OCEAN

Distribution of water masses

The vertical sections from 1984 indicated the presence of six water masses (Fig. 12) and from 1985 indicated the presence of four water masses (Fig. 13). From north to south, these strata were Subarctic Water, Transition Domain Water, the Subarctic Front, Transition Zone Water, the Subtropical Front, and Subtropical Water. Sampling in 1985 was not conducted far enough south detect the latter two water masses (Fig. 13).

Subarctic Water, which ranged from 55°N to 45°N in 1984 (Fig. 12) and from 55°N to 46°N in 1985 (Fig. 13), had a well-developed thermocline in the upper 50-75 m and a well-developed halocline in the upper 150 m. It was cool and of low salinity (< 32.8‰) overall and exhibited some upwelling on the temperature and sigma-t sections; upwelling also was indicated on the salinity section in 1985. This stratum had three subregions: low-salinity (approximately 32.5‰) Alaska Current System water between 55°N and 54°N in 1984 (absent in 1985), upwelling in the core of the Ridge Domain (approximately 54-49°N in 1984 and 55-49°N in 1985), and the eastward-flowing Subarctic Current System (49-45°N in 1984 and 49-46°N in 1985), which was bounded

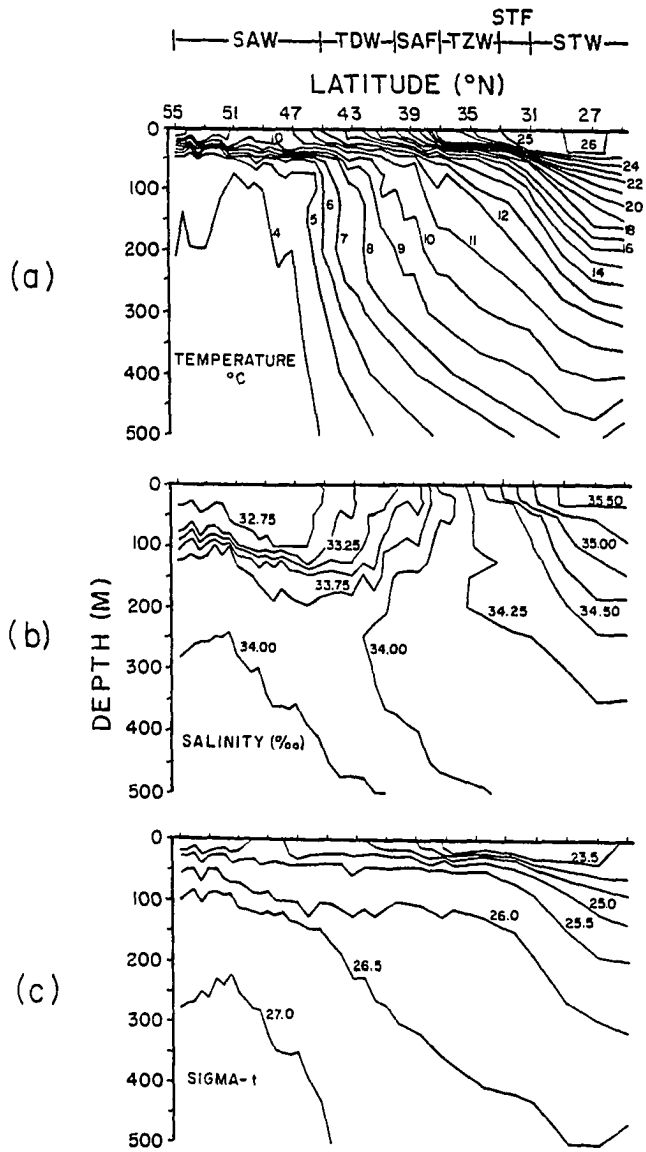

Figure 12. Vertical sections of (a) temperature, (b) salinity, and (c) sigma-t along 155°W in the northern North Pacific Ocean, 16 July-4 August 1984. (Data are from *Data Record of Oceanographic Observations and Exploratory Fishing* No. 28 [1985].) Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water; STF = Subtropical Front; STW = Subtropical Water.

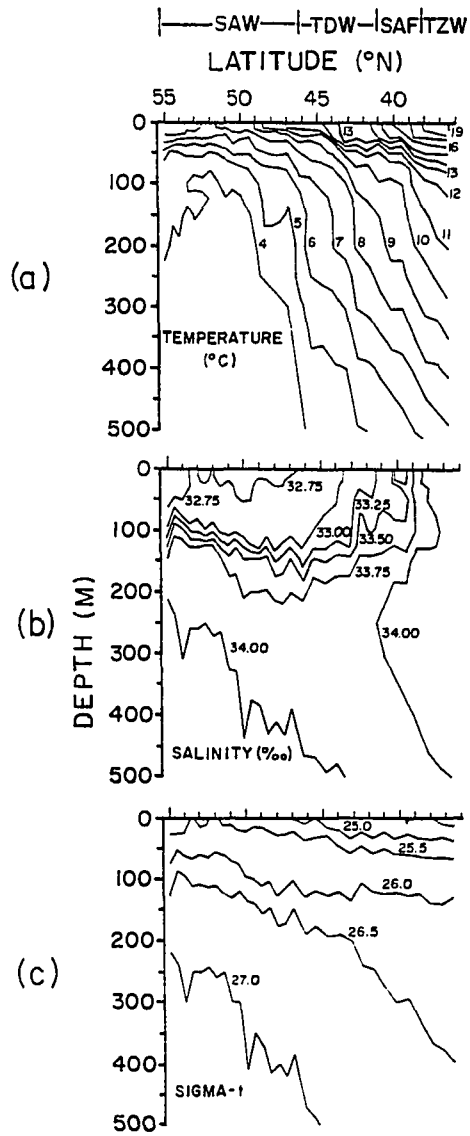

Figure 13. Vertical sections of (a) temperature, (b) salinity, and (c) sigma-t along 155°W in the northern North Pacific Ocean, 3-18 July 1985. (Data are from *Data Record of Oceanographic Observations and Exploratory Fishing* No. 29 [1986].) Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water.

to the north by the southern edge of the doming 4°C isotherm (see Dodimead *et al.* 1963 and Favorite *et al.* 1976).

Transition Domain Water is a water mass of changing (i.e., transitional) characteristics that lies along the southern edge of Subarctic Water (Dodimead *et al.* 1963, Favorite *et al.* 1976). It also is characterized by the presence of thermal inversions (Roden 1970; not shown in Figs. 12a and 13a), which occurred from 45°N to 40°N in 1984 and from 46°N to 41°N in 1985. In 1984, the thermocline in the Transition Domain decreased in strength (compared with that of waters both north and south of it), and the surface isotherms and isohalines exhibited a constant and slow change with latitude; further, the well-developed halocline seen farther north had broken down in this region. Transition Domain Water was not clearly defined in 1985, however, and did not exhibit the pronounced constant and slow change of surface isotherms and isohalines seen there in 1984 (Figs. 12a,b and 13a,b).

The Subarctic Front was clearly delineated by the abrupt change in both isotherms (approximately 5.2°C across the front in 1984 and 3.5°C across it in 1985) and isohalines (approximately 0.80‰ across the front in 1984 and 0.60‰ across it in 1985, with a complex salinity structure in the center of the front). This front lay between 40°N and 37°N in 1984 and between 41°N and 38°N in 1985 (Figs. 12 and 13). Ranges of both the temperature and salinity gradients in 1985 were approximately 70% those in 1984, indicating that the front was not as strongly developed in 1985. In both years, this large oceanic front was approximately 320 km (180 nm) wide in this part of the Pacific. The location and strength of this front vary with time, being dependent to a great extent on wind stress and Ekman transport (Roden 1972). One prominent feature of this frontal zone is that the area is characterized by hydrostatic instability, the strength of which varies

seasonally, being minimal during summer as a result of the formation of a shallow thermocline (Roden 1970, 1972).

Transition Zone Water occurs between the Subarctic Front and the Subtropical Front (Roden 1970, 1971, 1972) and was situated between approximately 37°N and 33°N in 1984 and between approximately 38°N and the southern end of the sampling line (36°30'N) in 1985 (Figs. 12 and 13). This region includes waters of both subtropical and subarctic origins (Roden 1970) and was indicated by a well-developed thermocline and a constant and slow change of surface isotherms with latitude.

The Subtropical Front, which is a salinity front only during the summer and fall (Roden 1974, 1980), was not distinct in the salinity section from 1984 (Fig. 12), probably because of the widely-spaced oceanographic sampling stations. It appeared, however, to lie in the vicinity of 33-31°N, where the surface salinity increased by approximately 0.5‰ in two degrees of latitude. Roden (1980) defined this front as incorporating the 34.80‰ isohaline, which also fell here. The Subtropical Front is narrow and extends across at least the western half of the North Pacific, between 28°N and 33°N. Unlike the Subarctic Front, it is weak; like the Subarctic Front, however, its north-south position varies with time, depending on wind stress and Ekman transport in the vicinity of the front itself. Its position also depends on the rate of evaporation in Subtropical Water south of it (Roden 1970, 1972). Finally, like the Subarctic Front, the Subtropical Front is characterized by hydrostatic instability (Roden 1970, 1972).

Subtropical Water lay south of the Subtropical Front in 1984 (Fig. 12), between approximately 31°N and at least the end of the sampling at 25°N. This water was both warm (> 25°C) and saline (> 35.00‰). This water type apparently extends as far south as the Doldrum Front, at approximately 11°N (Roden 1974).

Sea-surface temperatures along the transect line reflected the physical structure described above (Fig. 14a). In 1984, temperatures were high in northern Subarctic Water, decreased southward into the upwelling core of the Ridge Domain, and increased steadily southward from there to near the Subtropical Front. South of this front, sea-surface temperatures stabilized at approximately 26-27°C. A similar pattern in temperatures was seen in 1985, except that overall sea-surface temperatures were 1-4°C colder in 1985 and northern Subarctic Water was 3-4°C colder in 1985.

Sea-surface salinities also reflected the physical structure seen earlier (Fig. 14b). In 1984, sea-surface salinities were low in northern Subarctic Water, decreased only slightly southward in the upwelling core of the Ridge Domain, and steadily increased southward from there to near the Subtropical Front; south of this front, salinities stabilized at approximately 35.80‰. Salinities decreased slightly north of the Hawaiian Islands, perhaps due to freshwater input from rain along the northern coasts of those islands. Although the pattern of salinities in 1985 was similar to that seen in 1984, the 1985 salinities were higher by about 0.30‰.

Zooplankton

In both 1984 and 1985, the biomass of zooplankton in the upper 150 m of the water column was high in the Alaska Current System and northern Ridge Domain in northern Subarctic Water, low in the center of the Ridge Domain, and high in the Subarctic Current System and Transition Domain to approximately 42-41°N (Fig. 15, Table 5). In both years, the biomass was low from the Subarctic Front southward. In 1985, the zone of low biomass was in the center of the Ridge Domain and northern Transition Domain Water, between 49°N and 45°N.

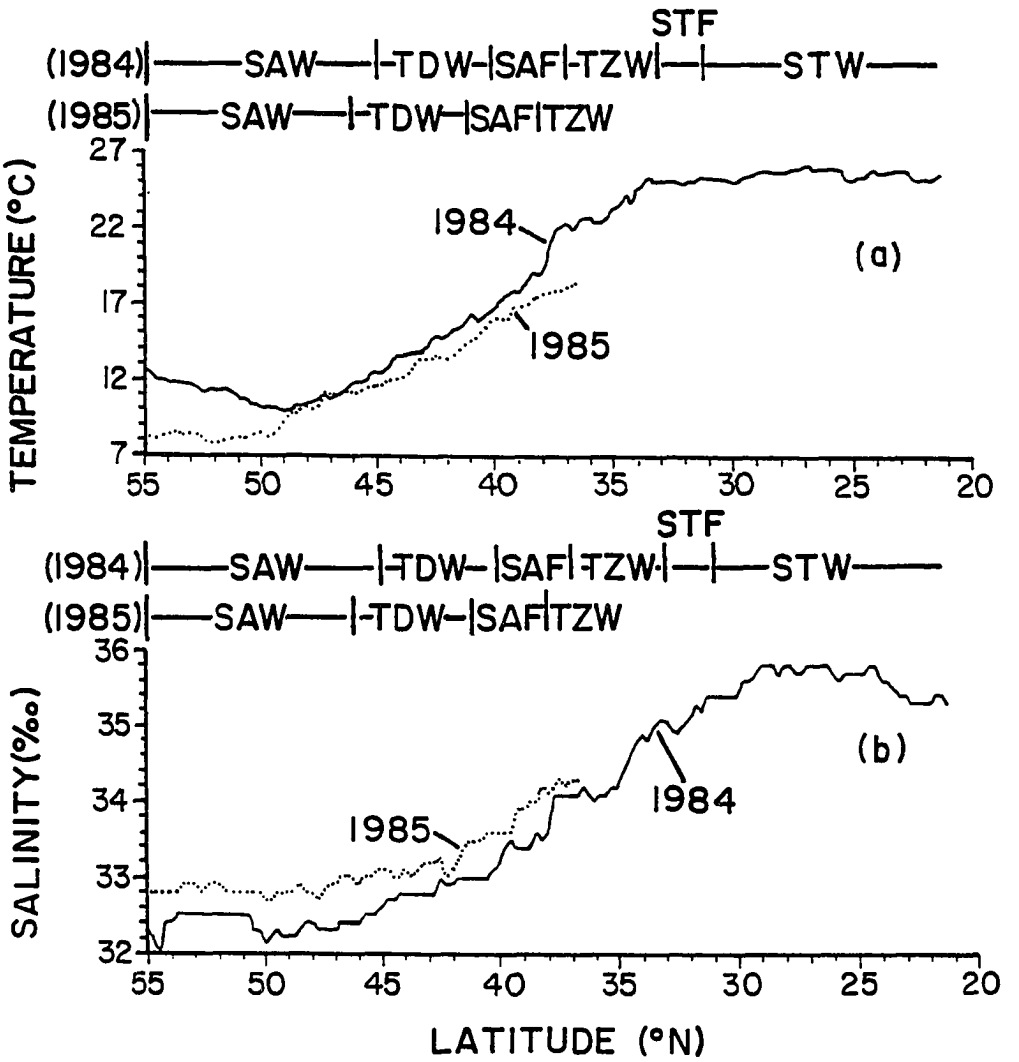

Figure 14. Sea-surface (a) temperatures and (b) salinities along 155°W in the northern North Pacific Ocean in 1984 (solid line) and 1985 (dotted line). Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water; STF = Subtropical Front; STW = Subtropical Water.

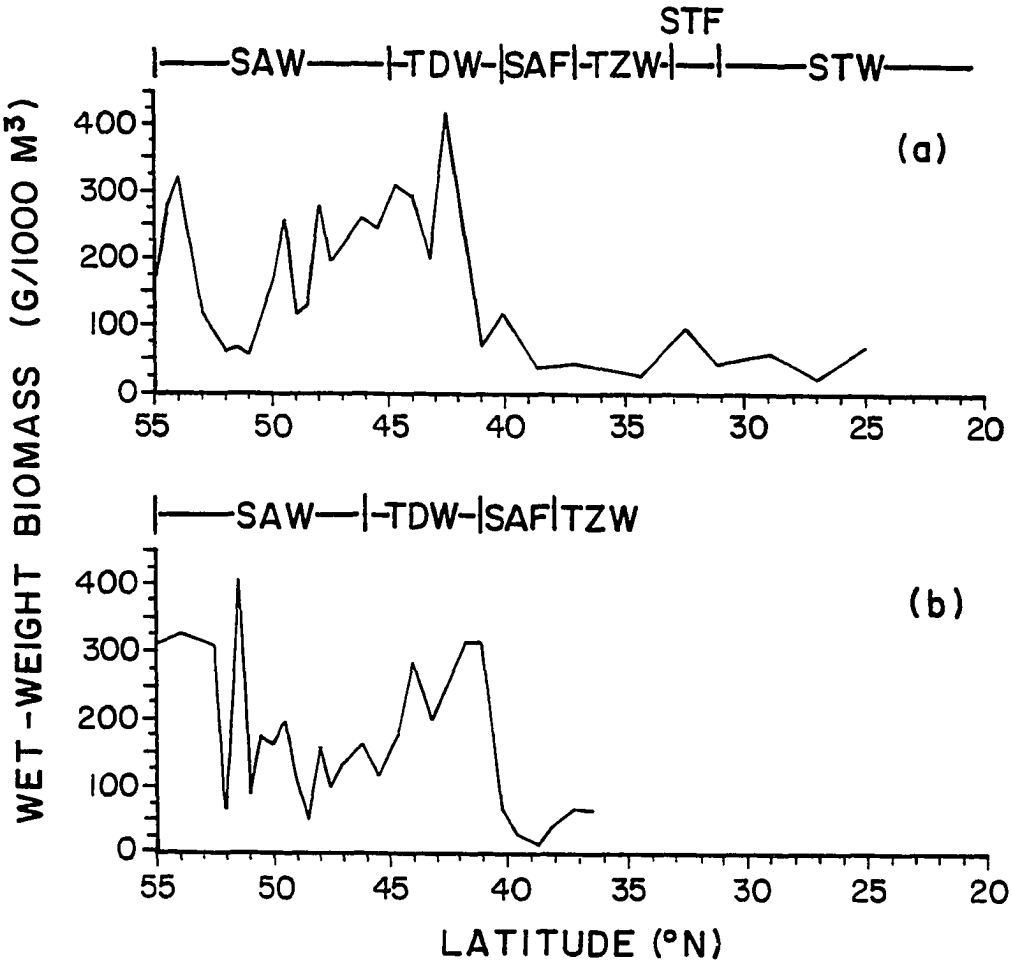

Figure 15. Variations in wet-weight biomass of zooplankton in the upper 150 m of the water-column along 155°W in the northern North Pacific Ocean in (a) 1984 and (b) 1985. (Data are from *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 [1985] and 29 [1986].) Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water; STF = Subtropical Front; STW = Subtropical Water.

Table 5. Wet-weight biomass (g/1000 m^3) of total zooplankton in five water masses along 155°W in the northern North Pacific Ocean during the summer of 1984 and in four water masses during the summer of 1985; samples were not collected in the Subtropical Front. (From *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 [1985] and 29 [1986].)

	Water mass														
	Subarctic Water			Transition Domain Water			Subarctic Front			Transition Zone Water			Subtropical Water		
Year	Mean	SE	(n)	Mean	SE	(n)	Mean	SE	(n)	Mean	SE	(n)	Mean	SE	(n)
1984	176.1	22.2	(16)	198.8	47.3	(5)	44.0	3.0	(2)	52.3	15.9	(4)	51.3	15.0	(3)
1985	178.6	26.3	(16)	226.2	39.9	(6)	28.3	8.7	(3)	66.0	0.7	(2)	-	-	(0)

The two-way ANOVA indicated that the biomass of zooplankton exhibited a water mass effect ($F = 6.971$; mean square error = 8091.087; $p < 0.05$; $df = 3, 45$), with Subarctic Water = Transition Domain Water > Subarctic Front = Transition Zone Water = Subtropical Front = Subtropical Water. (The latter two water masses were not sampled in 1985.) There was no year effect ($F = 0.134$; $p > 0.05$; $df = 1, 45$) or water mass-year interaction ($F = 0.085$; $p > 0.05$; $df = 3, 45$), indicating that the overall biomass did not differ between years and that the biomass was not concentrated in different water masses between years.

Fishes and squids

Most of the 20 primary species of fishes and squids caught in the gill-nets exhibited distinct relationships to water masses in both 1984 and 1985 (Fig. 16, Tables 6-8). The six species of eastern Pacific salmon (sockeye, chum, pink, coho, and chinook salmon, and steelhead), skilfish, and eight-armed squid were found throughout Subarctic Water. Of these eight species, only the skilfish appeared to avoid the coldest water in the upwelling core of the Ridge Domain. The boreal clubhook squid and the Pacific pomfret were found in both Subarctic Water and Transition Domain Water (the squid also occurred in low numbers in Transition Zone Water in 1985), but both were most abundant in southern Subarctic Water. CPUEs for nearly all species occurring primarily within Subarctic Water exhibited a significant water mass effect (Table 8), with the pattern for sockeye, chum, pink, and coho salmon, total salmon, and eight-armed squid being Subarctic Water > Transition Domain Water = Subarctic Front = Transition Zone Water. There was no year effect or water mass-year interaction for any of these species, indicating that overall CPUEs did not differ between years and that higher CPUEs did not occur in different water masses between years. CPUEs for skilfish, boreal clubhook

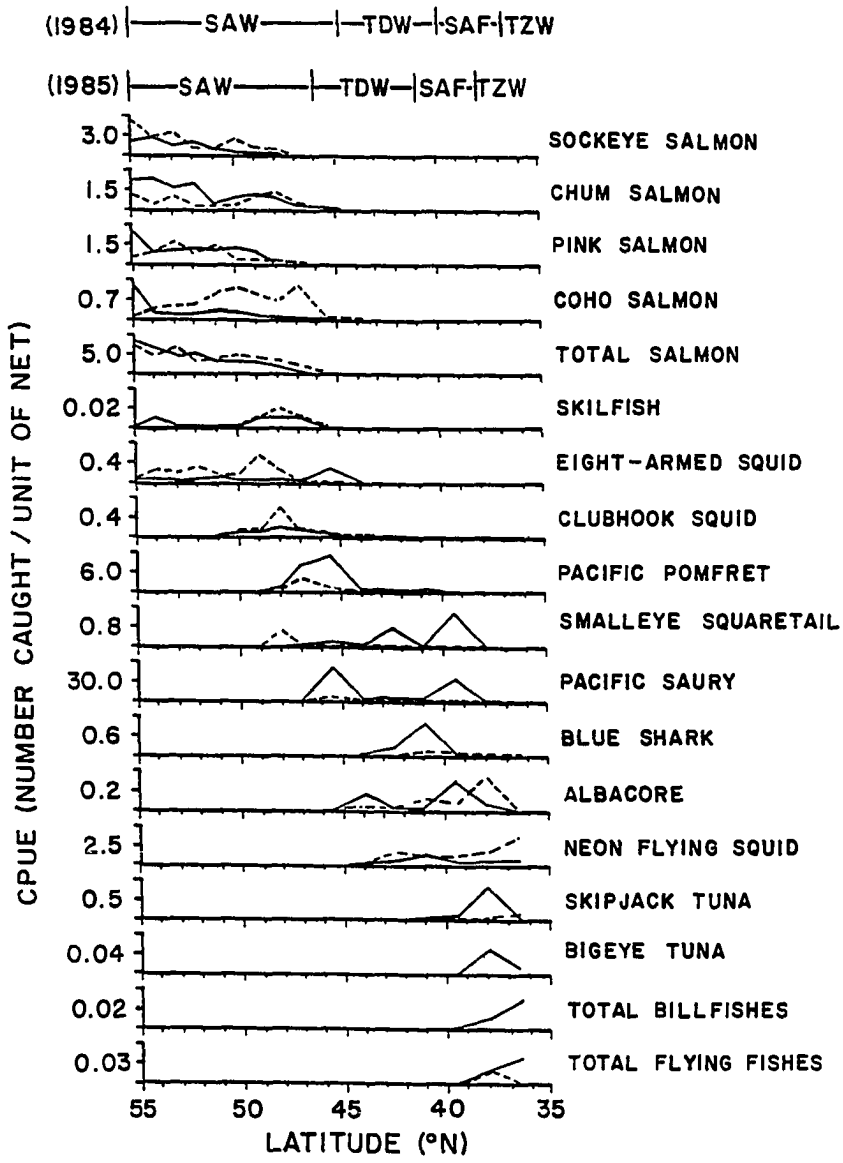

Figure 16. Variations in CPUEs of fishes and squids caught by gill-nets along 155°W in the northern North Pacific Ocean in 1984 (solid line) and 1985 (dashed line). (Data are from *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 [1985] and 29 [1986].) Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transitional Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water.

Table 6. CPUEs (number caught/unit of net) of fishes and squids in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1984. (From *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 [1985] and 29 [1986].)

	Water mass							
	Subarctic Water (n = 10)		Transition Domain Water (n = 3)		Subarctic Front (n = 2)		Transition Zone Water (n = 1)	
Species/taxon	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sockeye salmon	0.98	0.30	0	0	0	0	0	-
Chum salmon	1.20	0.27	0	0	0	0	0	-
Pink salmon	0.86	0.23	0	0	0	0	0	-
Coho salmon	0.23	0.10	0	0	0	0	0	-
Total salmon	3.38	0.82	0	0	0	0	0	-
Skilfish	< 0.01	< 0.01	0	0	0	0	0	-
Eight-armed squid	0.07	0.03	0	0	0	0	0	-
Boreal clubhook squid	0.05	0.02	0.01	0.01	0	0	0.01	-
Pacific pomfret	2.05	1.26	0.56	0.01	0.01	0.01	0	-
Smalleye squaretail	0.02	0.01	0.25	0.25	0.68	0.66	0	-
Pacific saury	5.02	5.02	2.46	1.37	16.33	16.29	0	-
Albacore	0	0	0.07	0.05	0.18	0.13	0	-
Blue shark	< 0.01	< 0.01	0.41	0.29	0	0	0	-
Neon flying squid	0	0	0.63	0.32	0.29	0.08	0.50	-
Skipjack tuna	0	0	0	0	0.43	0.38	0.03	-
Bigeye tuna	0	0	0	0	0.03	0.03	0.01	-
Total billfishes	0	0	0	0	0.01	< 0.01	0.03	-
Total flying fishes	0	0	0	0	0.01	0.01	0.04	-

Table 7. CPUEs (number caught/unit of net) of fishes and squids in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1985. (From *Data Record of Oceanographic Observations and Exploratory Fishing* Numbers 28 [1985] and 29 [1986].)

	Water mass							
	Subarctic Water (n = 10)		Transition Domain Water (n = 3)		Subarctic Front (n = 2)		Transition Zone Water (n = 1)	
Species/taxon	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sockeye salmon	1.73	0.51	0	0	0	0	0	-
Chum salmon	0.68	0.13	0	0	0	0	0	-
Pink salmon	0.61	0.18	0	0	0	0	0	-
Coho salmon	0.60	0.13	0	0	0	0	0	-
Total salmon	3.82	0.64	0	0	0	0	0	-
Skilfish	< 0.01	< 0.01	0	0	0	0	0	-
Eight-armed squid	0.18	0.05	0	0	0	0	0	-
Boreal clubhook squid	0.10	0.06	0.01	0.01	0	0	0	-
Pacific pomfret	0.45	0.36	0.22	0.19	0	0	0.09	-
Smalleye squaretail	0.06	0.06	0.01	0.01	0.01	0.01	0	-
Pacific saury	0.26	0.26	0.11	0.10	0.11	0.06	0.10	-
Albacore	0	0	0.06	0.03	0.20	0.15	0	-
Blue shark	0	0	0.03	0.03	0.03	0.02	0.01	-
Neon flying squid	0	0	0.90	0.39	1.28	0.28	3.57	-
Skipjack tuna	0	0	0	0	0	0	0.11	-
Bigeye tuna	0	0	0	0	0	0	0	-
Total billfishes	0	0	0	0	0	0	0	-
Total flying fishes	0	0	0	0	0.01	0.01	0	-

Table 8. F-statistics for two-way ANOVAs of CPUEs of fishes and squids in four water masses along 155°W in the northern North Pacific Ocean during the summers of 1984 and 1985.

Species/taxon	Year effect (df = 1, 24)[1]	Water mass effect (df = 3, 24)[1]	Water mass-year interaction (df = 3, 24)[1]	Mean square error
Sockeye salmon	0.114	3.541*	0.275	1.293
Chum salmon	0.215	6.835*	0.521	0.321
Pink salmon	0.047	4.158*	0.113	0.324
Coho salmon	0.339	4.241*	0.818	0.102
Total salmon	0.013	8.045*	0.031	4.027
Skilfish	0	1.412	0	< 0.001
Eight-armed squid	0.251	3.152*	0.607	0.013
Boreal clubhook squid	0.033	0.800	0.131	0.014
Pacific pomfret	0.139	0.446	0.206	6.414
Smalleye squaretail	2.930	1.669	2.381	0.066
Pacific saury	1.190	0.416	0.421	117.320
Albacore	0.003	10.501*	0.057	0.004
Blue shark	1.446	3.575*	2.902*	0.021
Neon flying squid	67.795*	46.248*	22.039*	0.072
Skipjack tuna	2.633	4.528*	4.684*	0.012
Bigeye tuna	6.083*	3.600*	3.600*	< 0.001
Total billfishes	152.069*	68.000*	68.000*	< 0.001
Total flying fishes	24.828*	20.000*	15.000*	< 0.001

[1] * = significant at $\alpha = 0.05$. Underlined values indicate the final result that was interpreted.

squid, and Pacific pomfret did not differ significantly among water masses, between years, or for a water mass-year interaction.

South of 45°N, three species concentrated in Transition Domain Water and were found across the Subarctic Front and into Transition Zone Water (Fig. 16, Tables 6-8). These three were the smalleye squaretail, Pacific saury, and albacore, which are primarily transitional-type species. The smalleye squaretail concentrated in southern Transition Domain Water and the Subarctic Front in 1984 and in southern Subarctic Water in 1985 but was primarily transitional and frontal in both years. The Pacific saury concentrated in southern Subarctic Water and around the Subarctic Front in 1984 but only in southern Subarctic Water in 1985. The albacore ranged from northern Transition Domain Water to Transition Zone Water and concentrated in or near the frontal zone in both years. CPUEs for only one of the three transitional species (albacore) exhibited a water mass effect (Table 8), with Transition Domain Water = Subarctic Front > Subarctic Water = Transition Zone Water. CPUEs for smalleye squaretail and Pacific saury did not differ significantly among water masses, between years, or for a water mass-year interaction.

At least eight species of fishes and squids were primarily transitional to tropical in occurrence in both years (Fig. 16, Tables 6-8). The blue shark, neon flying squid, skipjack tuna, bigeye tuna, total billfishes, and total flying fishes are subtropical and tropical species that occurred north to the Subarctic Front and, in some cases, into Transition Domain Water. In 1984, the blue shark even occurred as far north as the southern edge of Subarctic Water. CPUEs for all of these taxa exhibited a water mass-year interaction that actually consisted of primarily a year effect for four of the eight species (i.e., those species present in 1984 but absent or greatly reduced in numbers in 1985), with the blue shark exhibiting primarily a water mass effect and only the skipjack tuna exhibiting a true water mass-year interaction (Table 8). Most of these taxa occurred

primarily in the Subarctic Front and/or Transition Zone Water in both years or were in Transition Zone Water in 1984 but absent in 1985, suggesting that they occurred primarily farther south than sampling for fishes occurred in 1985.

Data on biomass were not collected for all fish and squid species, so exact determinations of the geographic distribution of fish and squid biomass were not possible. My impression, however, was that the pattern of biomass of fishes and squids was: Subarctic Water > Subarctic Front > or ≈ Transition Domain Water > Transition Zone Water.

Distribution of seabirds in water masses

Total densities of seabirds differed among water masses in both 1984 and 1985 (Figs. 17 and 18, Tables 9 and 10). Densities were highest in Subarctic Water, exhibiting peaks of 24.0 birds/km^2 in the core of upwelling in the Ridge Domain in 1984 and 28.5 birds/km^2 over the Subarctic Current System in 1985; these peaks consisted primarily of Short-tailed Shearwaters and Sooty Shearwaters, respectively. In contrast, densities in Transition Domain Water were < 1 bird/km^2 in 1984 and 1-2 birds/km^2 in 1985. Densities in and near the Subarctic Front were markedly higher than in the Transition Domain in 1984 (peak of 2.6 birds/km^2) but were only slightly higher in 1985 (peak of 0.9 birds/km^2). Densities were low in Transition Zone Water in both years (0.1 bird/km^2 in 1984 and 0.4 bird/km^2 in 1985). In 1984 (the only year of sampling), densities in the Subtropical Front and in northern Subtropical Water were < 0.1 bird/km^2, except within 200 km of the Hawaiian Islands, where they occurred in densities to 2.9 birds/km^2. Total densities differed significantly among water masses in 1984, with Subarctic Water > Subarctic Front > Transition Domain Water = Transition Zone Water =

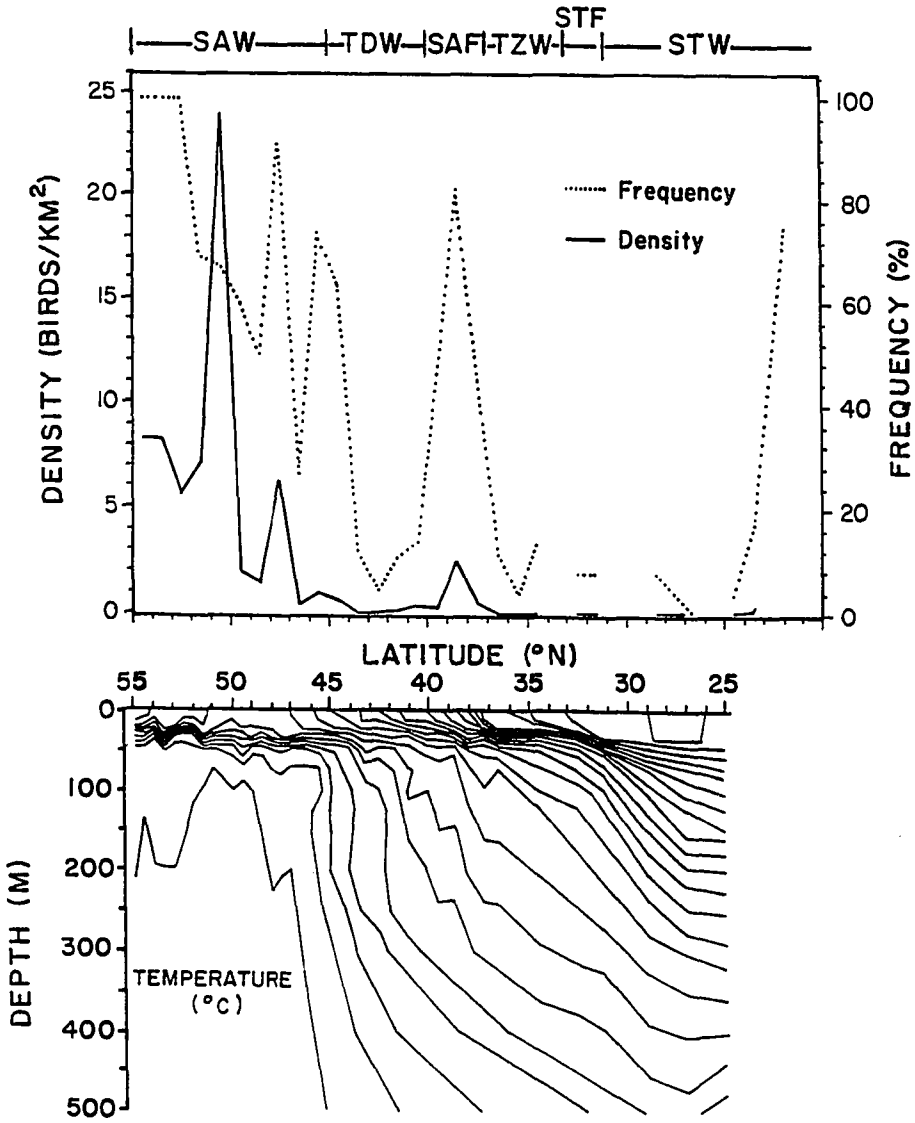

Figure 17. Variations in the total density and total frequency of occurrence of seabirds (top) along 155°W in the northern North Pacific Ocean in 1984 with respect to thermal structure (bottom). Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water; STF = Subtropical Front; STW = Subtropical Water.

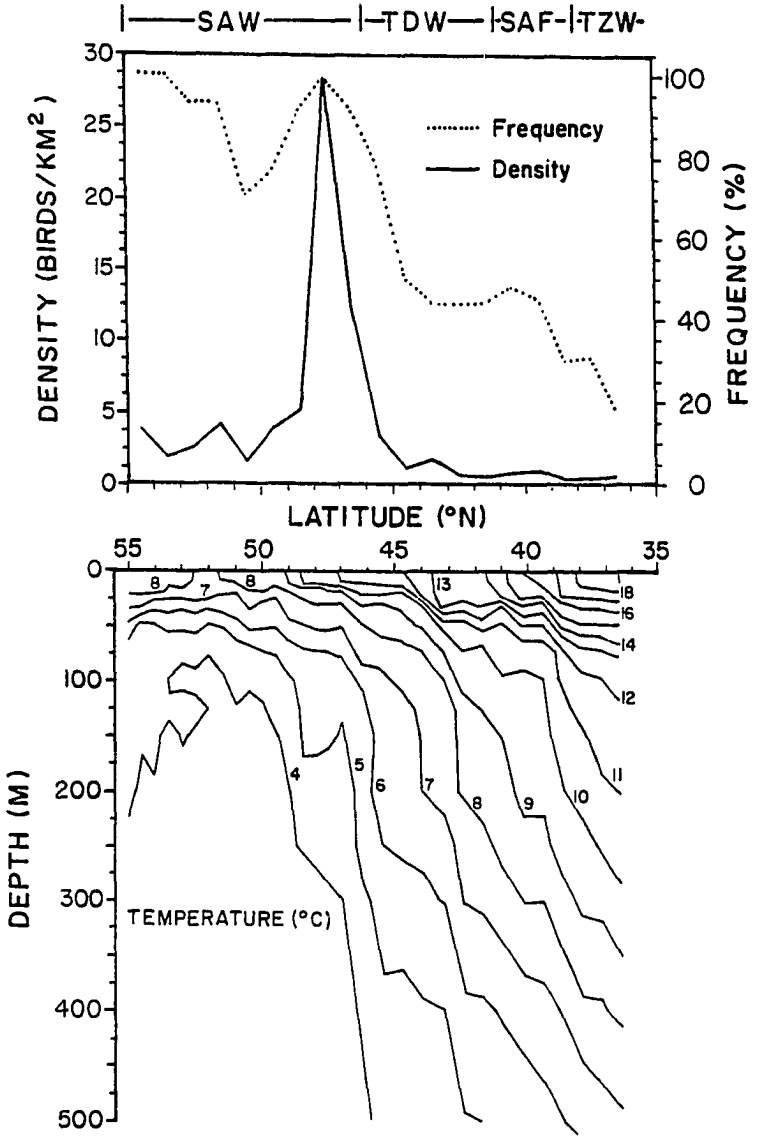

Figure 18. Variations in the total density and total frequency of occurrence of seabirds (top) along 155°W in the northern North Pacific Ocean in 1985 with respect to thermal structure (bottom). Abbreviations for water masses are: SAW = Subarctic Water; TDW = Transition Domain Water; SAF = Subarctic Front; TZW = Transition Zone Water.

Table 9. Densities (birds/km^2) of seabirds in six water masses along 155°W in the northern North Pacific Ocean during the summer of 1984.

	Water mass												
	Subarctic Water (n = 223)		Transition Domain Water (n = 116)		Subarctic Front (n = 69)		Transition Zone Water (n = 56)		Subtropical Front (n = 37)		Subtropical Water (n = 119)		Kruskal-Wallis H
Total density/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 5)[1]
TOTAL DENSITY	8.1	2.4	0.3	0.1	1.3	0.3	0.1	< 0.1	0.1	< 0.1	0.5	0.1	206.030*
Northern Fulmar	0.5	0.1	0	0	0	0	0	0	0	0	0	0	86.089*
Mottled Petrel	0.8	0.2	< 0.1	< 0.1	0	0	0	0	0	0	0	0	78.622*
Sooty Shearwater	0.8	0.2	0	0	0	0	0	0	0	0	0	0	88.140*
Short-tailed Shearwater	4.6	2.2	0	0	0	0	0	0	0	0	0	0	102.735*
Fork-tailed Storm-Petrel	0.3	0.1	< 0.1	< 0.1	0	0	0	0	0	0	0	0	70.390*
Pomarine Jaeger	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	3.566
Parasitic Jaeger	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	3.566
Long-tailed Jaeger	0.1	< 0.1	0	0	< 0.1	< 0.1	0	0	0	0	0	0	11.947*
Common Murre	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	1.780
Tufted Puffin	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	3.566
Buller's Shearwater	< 0.1	< 0.1	0	0	0	0	0	0	0	0	0	0	7.156
Laysan Albatross	< 0.1	< 0.1	0.1	< 0.1	0	0	0	0	0	0	0	0	15.879*†
Solander's Petrel	< 0.1	< 0.1	< 0.1	< 0.1	0	0	0	0	0	0	0	0	5.006
Black-footed Albatross	<0.1	< 0.1	< 0.1	< 0.1	0.1	< 0.1	< 0.1	< 0.1	0	0	0	0	10.423
Juan Fernandez Petrel	0	0	0	0	0.1	< 0.1	0	0	0	0	0	0	40.187*†
Cook's Petrel	0	0	0	0	0.1	< 0.1	0.1	< 0.1	0	0	0	0	24.271*†
Leach's Storm-Petrel	0.1	< 0.1	< 0.1	< 0.1	0.6	0.1	0	0	0	0	0	0	94.825*
Band-rumped Storm-Petrel	0	0	0	0	< 0.1	< 0.1	0	0	0	0	0	0	15.997*†
Sooty Storm-Petrel	0	0	0	0	< 0.1	< 0.1	0	0	0	0	0	0	7.986
Red Phalarope	< 0.1	< 0.1	0.2	0.1	0.3	0.1	0	0	0	0	0	0	35.437*†
Bulwer's Petrel	0	0	0	0	0	0	0	0	< 0.1	< 0.1	0.1	< 0.1	19.165*†
Red-tailed Tropicbird	0	0	0	0	0	0	0	0	< 0.1	< 0.1	0	0	15.757*†
Dark-rumped Petrel	< 0.1	< 0.1	< 0.1	< 0.1	0	0	0	0	0	0	< 0.1	< 0.1	12.954*†
Herald Petrel	0	0	0	0	0	0	0	0	0	0	< 0.1	< 0.1	4.210

Table 9. Densities (birds/km^2) of seabirds in six water masses along 155°W in the northern North Pacific Ocean during the summer of 1984 (continued).

	Water mass												
	Subarctic Water (n = 223)		Transition Domain Water (n = 116)		Subarctic Front (n = 69)		Transition Zone Water (n = 56)		Subtropical Front (n = 37)		Subtropical Water (n = 119)		Kruskal-Wallis H
Total density/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 5)[1]
Wedge-tailed Shearwater	0	0	0	0	0	0	0	0	0	0	0.2	0.1	42.718*†
Newell's Shearwater	0	0	0	0	0	0	0	0	0	0	< 0.1	< 0.1	4.210
White-tailed Tropicbird	0	0	0	0	0	0	0	0	0	0	< 0.1	< 0.1	4.210
Red-footed Booby	0	0	0	0	0	0	0	0	0	0	< 0.1	< 0.1	4.210
Sooty Tern	0	0	0	0	0	0	0	0	0	0	0.1	< 0.1	8.434
Brown Noddy	0	0	0	0	0	0	0	0	0	0	0.1	0.1	25.465*†

[1] * = significant at $\alpha = 0.05$; † = multiple comparisons revealed no significant pairwise differences in densities.

Table 10. Densities (birds/km^2) of seabirds in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1985.

	Water mass								
	Subarctic Water (n = 202)		Transition Domain Water (n = 131)		Subarctic Front (n = 83)		Transition Zone Water (n = 40)		Kruskal-Wallis H
Total density/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 3)[1]
TOTAL DENSITY	7.1	1.1	1.5	0.3	0.7	0.1	0.4	0.2	160.238*
Northern Fulmar	0.2	< 0.1	0	0	0	0	0	0	44.556*
Mottled Petrel	0.9	0.1	0.3	0.1	0	0	0	0	77.955*
Sooty Shearwater	5.0	1.1	0.5	0.2	0	0	0	0	74.981*
Short-tailed Shearwater	0.3	< 0.1	0	0	0	0	0	0	48.933*
Fork-tailed Storm-Petrel	0.3	0.1	0.3	0.3	0	0	0	0	41.709*
Pomarine Jaeger	< 0.1	< 0.1	0	0	0	0	0	0	2.520
Parasitic Jaeger	0	0	0	0	< 0.1	< 0.1	0.1	< 0.1	6.474
Long-tailed Jaeger	< 0.1	< 0.1	0	0	0	0	0	0	2.520
South Polar Skua	< 0.1	< 0.1	< 0.1	< 0.1	0	0	0	0	0.874
Black-legged Kittiwake	0.1	< 0.1	0	0	0	0	0	0	14.140*†
Tufted Puffin	< 0.1	< 0.1	0	0	0	0	0	0	7.628
Horned Puffin	< 0.1	< 0.1	0	0	0	0	0	0	1.257
Buller's Shearwater	< 0.1	< 0.1	0	0	0	0	< 0.1	< 0.1	4.819
Laysan Albatross	< 0.1	< 0.1	< 0.1	< 0.1	0	0	0	0	13.790*†
Solander's Petrel	< 0.1	< 0.1	0.1	< 0.1	< 0.1	< 0.1	0	0	8.068*†
Black-footed Albatross	< 0.1	< 0.1	0.1	< 0.1	0.1	< 0.1	0.1	< 0.1	8.356*†
Juan Fernandez Petrel	0	0	< 0.1	< 0.1	0.3	0.1	< 0.1	< 0.1	59.756*
Cook's Petrel	0	0	0	0	0.1	< 0.1	< 0.1	0.1	11.269*†
Leach's Storm-Petrel	0.3	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	0.1	< 0.1	33.796*

Table 10. Densities (birds/km^2) of seabirds in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1985 (continued).

	Water mass								
	Subarctic Water (n = 202)		Transition Domain Water (n = 131)		Subarctic Front (n = 83)		Transition Zone Water (n = 40)		Kruskal-Wallis H
Total density/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(df = 3)[1]
Band-rumped Storm-Petrel	0	0	0	0	< 0.1	< 0.1	0	0	4.494
Red Phalarope	0	0	0.1	< 0.1	0.2	0.1	0	0	16.549*†
Bulwer's Petrel	0	0	0	0	0	0	< 0.1	< 0.1	20.846*†
Herald Petrel	0	0	0	0	< 0.1	< 0.1	0	0	4.494

[1] * = significant at $\alpha = 0.05$; † = multiple comparisons revealed no significant pairwise differences in densities.

Subtropical Front = Subtropical Water. Total densities also differed significantly among water masses in 1985, with Subarctic Water > Transition Domain Water > Subarctic Front = Transition Zone Water. The two-way ANOVA indicated that there was a significant water mass-year interaction, probably because of the increase in densities in Transition Domain Water in 1985; the water mass effect was highly significant (much more so than the interaction was), however, suggesting that the differences in densities among water masses were real (Table 11). In addition, the year effect was more significant than the interaction and reflected the overall differences in densities between years.

Total frequencies of occurrence of seabirds per transect differed among water masses in both years (Figs. 17 and 18, Tables 12 and 13). Frequencies were 100% on transects nearest the shelf break of the northern Gulf of Alaska, low over the center of the Ridge Domain (to 50% in 1984 and 77% in 1985), and high again over the Subarctic Current System (to 91% in 1984 and 100% in 1985), where Sooty Shearwaters were most common. Frequencies increased further at the boundary between Subarctic Water and Transition Domain Water (sampled only in 1984), then much lower throughout Transition Domain Water (to 10% in 1984 and 40% in 1985). Frequencies were high in the Subarctic Front in 1984 (83%) but lower in 1985 (48%), then declined throughout Transition Zone Water (to 10% in 1984 and 20% in 1985). Frequencies were low (10-15%) in the Subtropical Front and in most of the Subtropical Water (both were sampled only in 1984), except near the Hawaiian Islands, where they increased to 74%. Total frequencies differed significantly among water masses in 1984, with Subarctic Water > Subarctic Front > Transition Domain Water > Subtropical Water > Transition Zone Water > Subtropical Front. The position of the Subtropical Water in this pattern was due primarily to high frequencies near the Hawaiian Islands. Total frequencies also

Table 11. F-statistics for two-way ANOVAs of densities of seabirds in four water masses along 155°W in the northern North Pacific Ocean during the summers of 1984 and 1985.

Total density/species	Year effect (df = 1, 912)[1]	Water mass effect (df = 3, 912)[1]	Water mass-year interaction (df = 3, 912)[1]	Mean square error
TOTAL DENSITY	6.836*	113.176*	4.721*	0.123
Northern Fulmar	1.220	27.361*	2.198	0.015
Mottled Petrel	5.706	38.174*	2.075	0.034
Sooty Shearwater	11.187*	35.584*	7.842*	0.079
Short-tailed Shearwater	3.389	26.570*	6.105*	0.047
Fork-tailed Storm-Petrel	1.065	19.809*	0.676	0.015
Pomarine Jaeger	0.018	1.466	0.032	0.001
Parasitic Jaeger	3.830	1.710	2.926*	< 0.001
Long-tailed Jaeger	1.420	2.890*	1.190	0.001
South Polar Skua	0.799	0.390	0.390	< 0.001
Black-legged Kittiwake	2.495	4.494*	4.494*	0.001
Common Murre	0.193	0.348	0.348	< 0.001
Tufted Puffin	0.579	3.064*	1.042	0.001
Horned Puffin	0.236	0.426	0.426	< 0.001
Buller's Shearwater	0.066	1.440	1.009	0.001
Laysan Albatross	0.433	6.161*	0.215	0.002
Solander's Petrel	3.450	2.304	1.999	0.002
Black-footed Albatross	2.860	2.155	1.685	0.005
Juan Fernandez Petrel	16.419*	29.589*	9.102*	0.003
Cook's Petrel	0.004	8.306*	0.002	0.002
Leach's Storm-Petrel	0.784	15.021*	23.711*	0.013
Band-rumped Storm-Petrel	0.791	5.452*	0.789	< 0.001
Sooty Storm-Petrel	2.044	2.039	2.039	< 0.001
Red Phalarope	1.681	12.203*	0.583	0.007
Bulwer's Petrel	12.620*	8.380*	8.380*	< 0.001
Dark-rumped Petrel	0.829	0.349	0.349	< 0.001
Herald Petrel	1.409	1.405	1.405	< 0.001

[1] * = significant at $\alpha = 0.05$. Underlined values indicate the final result that was interpreted.

Table 12. Frequencies of occurence (No.) and percent occurrences (%) of seabirds in six water masses along 155°W in the northern North Pacific Ocean during the summer of 1984. Results of χ^2 tests that included highly inflated χ^2 values from expected values < 5 are not presented.

	Water mass												
	Subarctic Water (n = 223)		Transition Domain Water (n = 116)		Subarctic Front (n = 69)		Transition Zone Water (n = 56)		Subtropical Front (n = 37)		Subtropical Water (n = 119)		χ^2
Total frequency/species	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	(df = 5)[1]
TOTAL FREQUENCY	160	71.7	24	20.7	39	56.5	5	8.9	3	8.1	22	18.5	179.44*
Northern Fulmar	47	21.1	0	0	0	0	0	0	0	0	0	0	90.46*
Mottled Petrel	41	18.4	1	0.9	0	0	0	0	0	0	0	0	74.61*
Sooty Shearwater	46	20.6	0	0	0	0	0	0	0	0	0	0	88.70*
Short-tailed Shearwater	52	23.3	0	0	0	0	0	0	0	0	0	0	101.08*
Fork-tailed Storm-Petrel	38	17.0	1	0.9	0	0	0	0	0	0	0	0	68.48*
Pomarine Jaeger	2	0.9	0	0	0	0	0	0	0	0	0	0	
Parasitic Jaeger	2	0.9	0	0	0	0	0	0	0	0	0	0	
Long-tailed Jaeger	5	2.2	0	0	1	1.4	0	0	0	0	0	0	
Common Murre	1	0.4	0	0	0	0	0	0	0	0	0	0	
Tufted Puffin	2	0.9	0	0	0	0	0	0	0	0	0	0	
Buller's Shearwater	4	1.8	0	0	0	0	0	0	0	0	0	0	
Laysan Albatross	5	2.2	7	6.0	0	0	0	0	0	0	0	0	
Solander's Petrel	4	1.8	1	0.9	0	0	0	0	0	0	0	0	
Black-footed Albatross	11	4.9	6	5.2	5	7.2	1	1.8	0	0	0	0	10.55
Juan Fernandez Petrel	0	0	0	0	5	7.2	0	0	0	0	0	0	
Cook's Petrel	0	0	0	0	3	4.3	3	5.4	0	0	0	0	
Leach's Storm-Petrel	18	8.1	1	0.9	22	31.9	0	0	0	0	0	0	92.54*
Band-rumped Storm-Petrel	0	0	0	0	2	2.9	0	0	0	0	0	0	
Sooty Storm-Petrel	0	0	0	0	1	1.4	0	0	0	0	0	0	
Red Phalarope	1	0.4	9	7.8	7	10.1	0	0	0	0	0	0	35.23*
Bulwer's Petrel	0	0	0	0	0	0	0	0	2	5.4	4	3.4	
Red-tailed Tropicbird	0	0	0	0	0	0	0	0	1	2.7	0	0	
Dark-rumped Petrel	1	0.4	1	0.9	0	0	0	0	0	0	5	4.2	
Herald Petrel	0	0	0	0	0	0	0	0	0	0	1	0.8	

Table 12. Frequencies of occurence (No.) and percent occurrences (%) of seabirds in six water masses along 155°W in the northern North Pacific Ocean during the summer of 1984 (continued).

	Water mass												
	Subarctic Water (n = 223)		Transition Domain Water (n = 116)		Subarctic Front (n = 69)		Transition Zone Water (n = 56)		Subtropical Front (n = 37)		Subtropical Water (n = 119)		χ^2
Total frequency/species	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	(df = 5)[1]
Wedge-tailed Shearwater	0	0	0	0	0	0	0	0	0	0	10	8.4	
Newell's Shearwater	0	0	0	0	0	0	0	0	0	0	1	0.8	
White-tailed Tropicbird	0	0	0	0	0	0	0	0	0	0	1	0.8	
Red-footed Booby	0	0	0	0	0	0	0	0	0	0	1	0.8	
Sooty Tern	0	0	0	0	0	0	0	0	0	0	2	1.7	
Brown Noddy	0	0	0	0	0	0	0	0	0	0	6	5.0	

[1] * = significant at $\alpha = 0.05$.

Table 13. Frequencies of occurrence (No.) and percent occurrences (%) of seabird species in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1985. Results of χ^2 tests that included highly inflated χ^2 values from expected values < 5 are not presented.

	Water mass								
	Subarctic Water (n = 202)		Transition Domain Water (n = 131)		Subarctic Front (n = 83)		Transition Zone Water (n = 40)		χ^2
Total frequency/species	No.	%	No.	%	No.	%	No.	%	(df = 3)[1]
TOTAL FREQUENCY	185	91.6	68	51.9	34	41.0	11	27.5	118.69*
Northern Fulmar	34	16.8	0	0	0	0	0	0	46.10*
Mottled Petrel	82	40.6	22	16.8	0	0	0	0	75.19*
Sooty Shearwater	77	38.1	17	13.0	0	0	0	0	74.44*
Short-tailed Shearwater	26	12.9	0	0	0	0	0	0	37.46*
Fork-tailed Storm-Petrel	45	22.3	7	5.3	0	0	0	0	44.40*
Pomarine Jaeger	2	1.0	0	0	0	0	0	0	
Parasitic Jaeger	0	0	0	0	1	1.2	1	2.5	
Long-tailed Jaeger	2	1.0	0	0	0	0	0	0	
South Polar Skua	1	0.5	1	0.8	0	0	0	0	
Black-legged Kittiwake	11	5.4	0	0	0	0	0	0	14.59*
Tufted Puffin	6	3.0	0	0	0	0	0	0	
Horned Puffin	1	0.5	0	0	0	0	0	0	
Buller's Shearwater	1	0.5	0	0	0	0	1	2.5	
Laysan Albatross	1	0.5	7	5.3	0	0	0	0	
Solander's Petrel	5	2.5	8	6.1	1	1.2	0	0	
Black-footed Albatross	6	3.0	13	9.9	7	8.4	3	7.5	7.39
Juan Fernandez Petrel	0	0	3	2.3	17	20.5	1	2.5	59.75*
Cook's Petrel	0	0	0	0	3	3.6	1	2.5	
Leach's Storm-Petrel	44	21.8	4	3.1	3	3.6	5	12.5	33.09*

Table 13. Frequencies of occurrence (No.) and percent occurrences (%) of seabird species in four water masses along 155°W in the northern North Pacific Ocean during the summer of 1985 (continued).

	Water mass								
	Subarctic Water (n = 202)		Transition Domain Water (n = 131)		Subarctic Front (n = 83)		Transition Zone Water (n = 40)		χ^2
Total frequency/species	No.	%	No.	%	No.	%	No.	%	(df = 3)[1]
Band-rumped Storm-Petrel	0	0	0	0	1	1.2	0	0	
Red Phalarope	0	0	8	6.1	6	7.2	0	0	16.82*
Bulwer's Petrel	0	0	0	0	0	0	2	5.0	
Herald Petrel	0	0	0	0	1	1.2	0	0	

[1] * = significant at $\alpha = 0.05$.

differed significantly among water masses in 1985, with Subarctic Water > Transition Domain Water > Subarctic Front > Transition Zone Water.

Northern Fulmars occurred only in Subarctic Water and as far south as 50°N in both years (Figs. 19 and 20, Tables 9 and 10). Densities were highest in northern Subarctic Water (2.5 birds/km^2 in 1984 and 1.1 birds/km^2 in 1985) and decreased quickly to zero, indicating this species' affinity for waters of the shelf and shelf break in the northern Gulf of Alaska. Densities differed significantly among water masses in both years, with Subarctic Water > all other water masses. There was a significant water mass effect, reflecting this species' affinity for Subarctic Water (Table 11). Frequencies also differed significantly among water masses in both years and followed the pattern seen for densities (Tables 12 and 13).

Mottled Petrels concentrated in Subarctic Water (primarily over the Ridge Domain) in both years but also occurred as far south as central (1984) to southern (1985) Transition Domain Water (Figs. 19 and 20, Tables 9 and 10). Highest densities were 6.0 birds/km^2 in 1984 and 2.4 birds/km^2 in 1985, both over the Ridge Domain; secondary peaks in densities occurred over the Subarctic Current System in both years. Densities differed significantly among water masses in 1984, with Subarctic Water > all other water masses; densities also differed significantly among water masses in 1985, with Subarctic Water > Transition Domain Water > Subarctic Front = Transition Zone Water. There was a significant water mass effect, reflecting this species' affinity for Subarctic and (secondarily) Transition Domain waters (Table 11). Frequencies also differed significantly among water masses in both years, with this species recorded almost entirely in Subarctic Water (Tables 12 and 13).

Sooty Shearwaters occurred only in Subarctic Water in 1984 but ranged throughout Subarctic Water and south to northern Transition Domain Water in 1985; peak

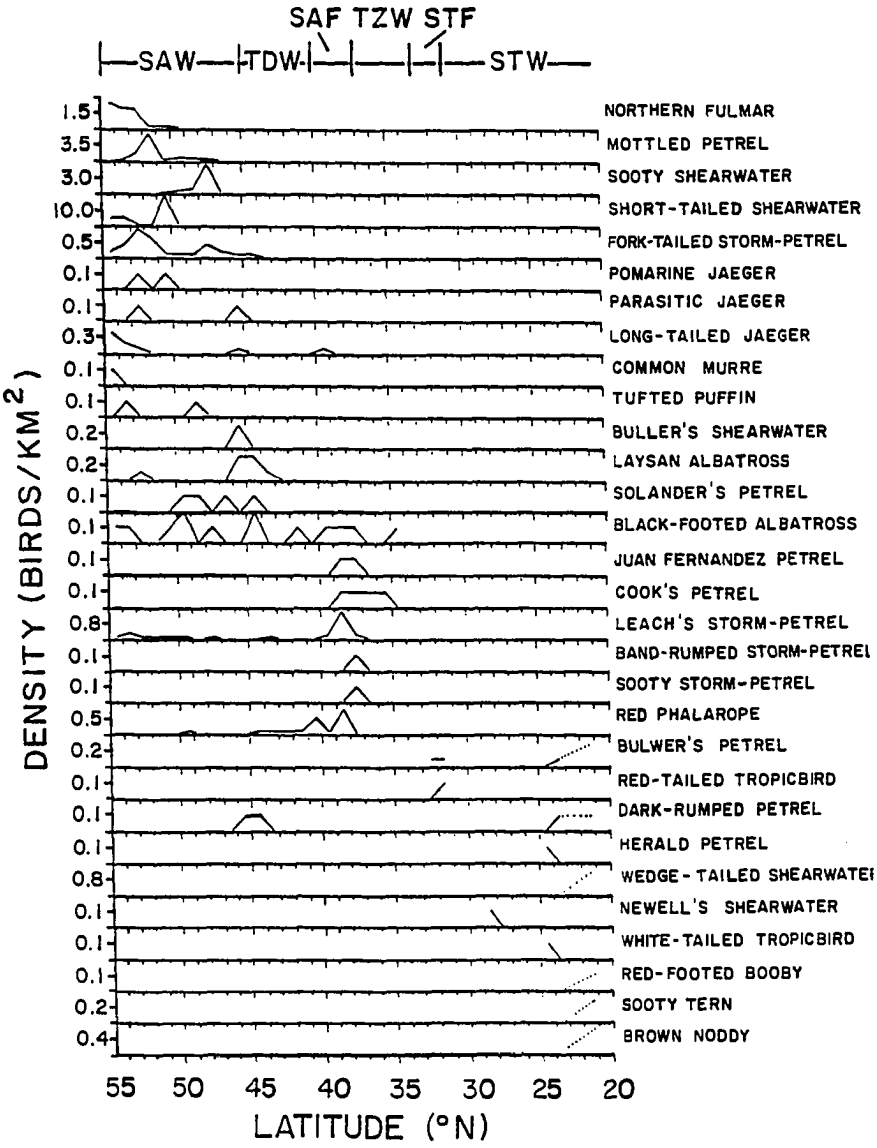

Figure 19. Variation in densities of seabirds along 155°W in the northern North Pacific Ocean in 1984. Abbreviations for water masses are as in Figure 17. Dotted lines represent values between a sample at 23-24°N and a sample at 21-22°N.

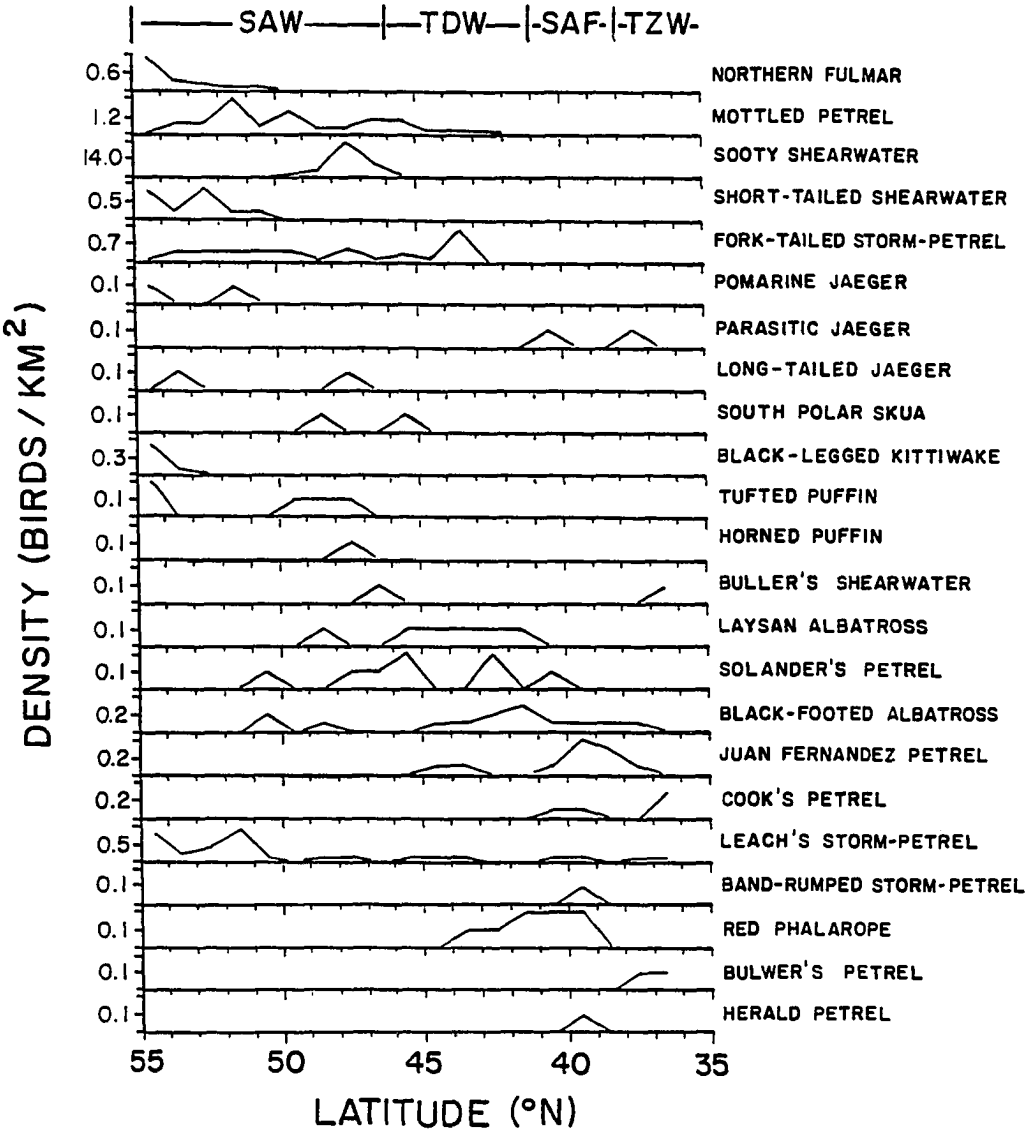

Figure 20. Variation in densities of seabirds along 155°W in the northern North Pacific Ocean in 1985. Abbreviations for water masses are as in Figure 18.

densities occurred over the Subarctic Current System in both 1984 (5.5 birds/km^2) and 1985 (27.2 birds/km^2; Figs. 19 and 20, Tables 9 and 10). This was one of the few species that occurred over the entire latitudinal range of Subarctic Water, although densities were very low over most of that range. Densities differed significantly among water masses in both years, with Subarctic Water > all other water masses. There was a significant water mass-year interaction, probably because of the records in Transition Domain Water in 1985; the water mass effect was highly significant (much more so than the interaction), however, suggesting that the differences in densities among water masses were real (Table 11). In addition, the year effect was more significant than the interaction and reflected the increase in densities in 1985. Frequencies differed significantly among water masses in both years, with Subarctic Water > all other water masses (Tables 12 and 13).

Short-tailed Shearwaters concentrated only in Subarctic Water in both years, although densities were much higher overall in 1984 than in 1985 (Figs. 19 and 20, Tables 9 and 10). Peak densities occurred over the upwelling center of the Ridge Domain in both 1984 (19.2 birds/km^2) and 1985 (0.9 birds/km^2); densities also were moderate to high at the northern edge of the study area in both years. Densities differed significantly among water masses in both years, with Subarctic Water > all other water masses. There was a significant, but spurious, water mass-year interaction: this species used the same water mass in both years (Table 11). Perhaps the large interannual differences in densities caused this spurious result. The water mass effect was highly significant (much more so than the interaction), however, suggesting that the differences in densities among water masses were real. Frequencies also differed significantly among water masses, with the pattern following that seen for densities (Tables 12 and 13).

Fork-tailed Storm-Petrels occurred primarily in Subarctic Water in both years, with birds recorded south to northern (1984) or central (1985) Transition Domain Water. Densities were highest over the northern part of the Alaska Gyre in 1984 (0.9 birds/km^2) and over Transition Domain Water (1.3 birds/km^2) in 1985 (Figs. 19 and 20, Tables 9 and 10). In 1984, a secondary concentration occurred over the Subarctic Current System, in the area where Sooty Shearwaters concentrated. Densities differed significantly among water masses in both years, with Subarctic Water > all other water masses. There was a significant water mass effect, reflecting this species' affinity for Subarctic and (secondarily) Transition Domain waters (Table 11). Frequencies also differed significantly among water masses, with the pattern following that seen for densities (Tables 12 and 13).

Pomarine Jaegers were seen only in Subarctic Water in both years, occurring only over the upwelling core of the Ridge Domain (both years) and near the shelf break (1985 only; Figs. 19 and 20, Tables 9 and 10). Densities and frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 9-10 and 12-13). There were no year or water mass effects and no water mass-year interaction (Table 11).

Parasitic Jaegers were seen only in Subarctic Water in 1984, occurring over the upwelling core of the Ridge Domain and near the southern edge of Subarctic Water (Fig. 19, Table 9). In contrast to their 1984 distribution, Parasitic Jaegers in 1985 occurred only in the Subarctic Front and in Transition Zone Water immediately south of it (Fig. 20, Table 10). Densities and frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 9-10 and 12-13). In contrast, the water mass-year interaction indicated a real difference in distribution between years (Table 11).

Long-tailed Jaegers occurred in Subarctic Water (primarily near the shelf break) in both years but also occurred in low densities at the southern edge of Subarctic Water (both years) and in the Subarctic Front (1984 only; Figs. 19 and 20, Tables 9 and 10). Densities in 1984 appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences (Table 9). Densities (1985) and frequencies (both years) were extremely low everywhere and did not differ significantly among water masses (Tables 10, 12, and 13). In contrast, there was a significant water mass effect, reflecting this species' affinity for Subarctic Water (Table 11).

South Polar Skuas were recorded only in 1985, in southern Subarctic Water (over the Subarctic Current System) and just south of the boundary between Subarctic Water and Transition Domain Water (Fig. 20, Table 10). This species occurs in low numbers around concentrations of other birds, from the Subarctic Current System south to the Subarctic Front (Day, unpubl. data). Densities and frequencies were extremely low everywhere and did not differ significantly among water masses (Tables 10 and 13), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Black-legged Kittiwakes were recorded only in 1985, occurring only in Subarctic Water at the northern edge of the study area; they were not recorded south of 53°N (Fig. 20, Table 10). Densities appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences. In contrast, frequencies differed significantly among water masses and indicated this species' preference for Subarctic Water (Table 13). There was a significant, but spurious, water mass-year interaction (Table 11). The interannual differences in densities probably caused this spurious result. The water mass effect was as significant as the interaction, however, suggesting that the differences in densities among water masses were real.

Common Murres were seen only in 1984, over the Alaska Current System in Subarctic Water (Fig. 19, Table 9). Densities and frequencies were extremely low everywhere and did not differ significantly among water masses (Tables 9 and 12). There were no year or water mass effects and no water mass-year interaction (Table 11).

Tufted Puffins occurred only in Subarctic Water in both years, both near land and over the Subarctic Current System (Figs. 19 and 20, Tables 9 and 10). Although the adult-plumaged birds at the northern end of the study area might have been foraging breeders, the southern birds were subadults by plumage. Densities and frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 9-10 and 12-13). In contrast, there was a significant water mass effect, reflecting this species' affinity for Subarctic Water (Table 11).

Horned Puffins were recorded only in 1985 and occurred only over the Subarctic Current System, in southern Subarctic Water (Fig. 20, Table 10). These birds were subadults by plumage. Densities and frequencies were extremely low everywhere and did not differ significantly among water masses (Tables 10 and 13), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Buller's Shearwaters occurred only in southern Subarctic Water in 1984, over the southern Subarctic Current System and near the boundary with Transition Domain Water. In contrast, they occurred as single birds in two disparate locations in 1985, one in southern Subarctic Water and the other in Transition Zone Water (Figs. 19 and 20, Tables 9 and 10). This latter record is the only time I have ever recorded this species, which occurs primarily from southern Subarctic Water to the Subarctic Front, in this water mass (Day, unpubl. data). Densities and frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 9-10 and 12-13), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Laysan Albatrosses occurred in Subarctic Water and Transition Domain Water in both years, with densities in 1984 highest at the boundary between Subarctic Water and Transition Domain Water (0.3 birds/km^2). Densities in 1985 were low and uniform in southern Subarctic Water and throughout Transition Domain Water (Figs. 19 and 20, Tables 9 and 10). Densities in both years appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences, probably because most birds occurred at the boundary between two water masses (Tables 9 and 10). Frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 12 and 13). In contrast, there was a significant water mass effect, reflecting this species' affinity for Subarctic and Transition Domain waters (Table 11).

Solander's Petrels were birds primarily of southern Subarctic Water and Transition Domain Water. They concentrated over the Subarctic Current System in 1984 and from the southern edge of Subarctic Water to central Transition Domain Water in 1985 (Figs. 19 and 20, Tables 9 and 10). Densities in 1985 appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences (Table 10). Densities (1984 only) and frequencies (both years) were extremely low everywhere and did not differ significantly among water masses (Tables 9, 12, and 13), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Black-footed Albatrosses occurred widely from Subarctic Water to Transition Zone Water in both years. Although densities were low overall, they were highest over the center of the Ridge Domain and at boundaries between water masses (Subarctic Water and Transition Domain Water in 1984, Transition Domain Water and the Subarctic Front in 1985; Figs. 19 and 20, Tables 9 and 10). Densities appeared to differ significantly

among water masses in 1985, but multiple comparisons revealed no significant pairwise differences (Table 10). Densities (1984 only) and frequencies (both years) were extremely low everywhere and did not differ significantly among water masses (Tables 9, 12, and 13), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Juan Fernandez Petrels occurred only within the Subarctic Front in 1984 and primarily there in 1985; they also occurred in southern Transition Domain Water and in northern Transition Zone Water in 1985 (Figs. 19 and 20, Tables 9 and 10). Densities appeared to differ significantly among water masses in both years, but multiple comparisons revealed no significant pairwise differences in 1984; the pattern in 1985 was Subarctic Front > all other water masses. There was a significant water mass-year interaction, probably because of the records outside of the Subarctic Front in 1985. The water mass effect was highly significant (much more so than the interaction), however, indicating that the affinity for the Subarctic Front was real (Table 11). In addition, the year effect was more significant than the interaction and reflected the increase in densities in 1985. Frequencies did not differ in 1984 but differed significantly among water masses in 1985, with the pattern following that seen for densities (Tables 12 and 13).

Cook's Petrels occurred in low densities in the Subarctic Front and in Transition Zone Water just south of the front in both years (Figs. 19 and 20, Tables 9 and 10). Densities appeared to differ significantly among water masses in both years, but multiple comparisons revealed no significant pairwise differences. There was a significant water mass effect, reflecting this species' affinity for Subarctic Front and Transition Zone waters (Table 11). In contrast, frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 12 and 13).

Leach's Storm-Petrels occurred widely from Subarctic Water to the Subarctic Front in both years; densities were high only in the Subarctic Front in 1984 (1.4 birds/km^2) and over the core of the Ridge Domain in 1985 (0.9 birds/km^2; Figs. 19 and 20, Tables 9 and 10). Densities differed significantly among water masses in both years, with Subarctic Front > all other water masses in 1984; the pattern for 1985 was Subarctic Water > Transition Domain Water = Subarctic Front, Subarctic Water = Transition Zone Water (probably because of the small sample size in the latter water mass), and Transition Zone Water = Transition Domain Water = Subarctic Front. There was a significant water mass-year interaction that indicated a real difference in distribution between years (Table 11). Following the patterns seen for densities, frequencies were highest in the Subarctic Front in 1984 and in Subarctic Water in 1985 (Tables 12 and 13).

The Band-rumped Storm-Petrel was a primarily subtropical species that occurred only at the Subarctic Front in both years (Figs. 19 and 20, Tables 9 and 10). It breeds in the Hawaiian Islands and apparently flies north to feed at the front. Densities appeared to differ significantly among water masses in 1984, but multiple comparisons revealed no significant pairwise differences (Table 9). Densities (1985) and frequencies (both years) were extremely low everywhere and did not differ significantly among water masses (Tables 10, 12, and 13). In contrast, there was a significant water mass effect, reflecting this species' affinity for the Subarctic Front (Table 11).

The Sooty Storm-Petrel was a primarily subtropical species that was seen only in 1984, at the Subarctic Front (Fig. 19, Table 9). It breeds in the Hawaiian Islands and apparently flies north to feed at the front. Densities and frequencies were extremely low everywhere and did not differ significantly among water masses (Tables 9 and 12), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Red Phalaropes were recorded primarily in southern Transition Domain Water and the Subarctic Front in both years; they also occurred once in Subarctic Water in 1984 (Figs. 19 and 20, Tables 9 and 10). This species and the Leach's Storm-Petrel were the most abundant birds in the Subarctic Front. Densities appeared to differ significantly among water masses in both years, but multiple comparisons revealed no significant pairwise differences. There was a significant water mass effect, however, reflecting this species' affinity for Subarctic Front and (secondarily) Transition Domain waters (Table 11). Frequencies also were higher in the Subarctic Front and Transition Domain Water than in other water masses (Tables 12 and 13).

Bulwer's Petrels occurred only in the Subtropical Front and in Subtropical Water in 1984, with highest densities near the Hawaiian Islands. They were recorded only two times in 1985, both in Transition Zone Water (Figs. 19 and 20, Tables 9 and 10). This species normally ranges north from Subtropical Water to the Subarctic Front, however (Day, unpubl. data). Densities appeared to differ significantly among water masses in both years, but multiple comparisons revealed no significant pairwise differences. There was a significant, but spurious, water mass-year interaction: this species used the same water mass in both years. The interannual differences in densities may have caused this spurious result (Table 11). The year effect was more significant than the interaction, however, and reflected real interannual differences in densities. Frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 12 and 13).

Red-tailed Tropicbirds were exclusively warm-water birds that were seen only in 1984, in the Subtropical Front (Fig. 19, Table 9). This species was not recorded on transects south of there but was seen off transect in very low numbers south to the Hawaiian Islands. Densities appeared to differ significantly among water masses, but

multiple comparisons revealed no significant pairwise differences. Frequencies were extremely low everywhere and did not differ significantly among water masses (Table 12). A two-way ANOVA could not be calculated for this species, because it was seen only in one of the southernmost two water masses in 1984.

Dark-rumped Petrels were recorded in three disparate water masses in 1984: on both sides of the boundary between southern Subarctic Water and northern Transition Domain Water and in Subtropical Water (Fig. 19, Table 9). The former two records constitute the first records of this species outside of its normally subtropical range and are far north of its Hawaiian Islands breeding grounds (King 1970, American Ornithologists' Union 1983). Indeed, these are the only unusual records that I have for the distribution of this species in over 11,000 transect stations. The other, more typical records occurred between 23°N and 21°N, which seems to be the normal at-sea range north of the Hawaiian Islands (King 1970). Densities appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences. Frequencies were extremely low everywhere and did not differ significantly among water masses (Table 12), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Herald Petrels were recorded only once each year, in Subtropical Water (1984) and the Subarctic Front (1985; Figs. 19 and 20, Tables 9 and 10). They normally range northward in very low densities to the Subarctic Front, however (Day, unpubl. data). Densities and frequencies were extremely low everywhere in both years and did not differ significantly among water masses (Tables 9 and 12), and there were no year or water mass effects and no water mass-year interaction (Table 11).

Wedge-tailed Shearwaters were recorded only in 1984, in Subtropical Water near the Hawaiian Islands (Fig. 19, Table 9). Elsewhere in Subtropical Water, this species

forages within approximately 100 km of nesting islands (King 1970; Day, unpubl. data). Densities appeared to differ among water masses, but multiple comparisons revealed no significant pairwise differences. Frequencies were too low overall to detect differences, although this species occurred on 52.6% of the transect stations near the Hawaiian Islands (Table 12). A two-way ANOVA could not be calculated for this species.

Newell's Shearwaters and White-tailed Tropicbirds were recorded only once each in 1984, in Subtropical Water in the zones 29-28°N and 25-24°N, respectively (Fig. 19, Table 9). The former zone is an area where small, microscale convergences occurred at the surface, and much flotsam and jetsam was trapped there. Densities and frequencies were extremely low everywhere and did not differ significantly among water masses (Tables 9 and 12). Two-way ANOVAs could not be calculated for these species.

Red-footed Boobies, Sooty Terns, and Brown Noddies were recorded only in 1984, in Subtropical Water just off the Hawaiian Islands (Fig. 19, Table 9). The boobies and noddies are true nearshore feeders in Subtropical Water (Day, unpubl. data). Densities of the booby and tern and frequencies of all three species were extremely low everywhere and did not differ significantly among water masses. Densities of the noddies appeared to differ significantly among water masses, but multiple comparisons revealed no significant pairwise differences (Tables 9 and 12). Two-way ANOVAs could not be calculated for these species.

DISCUSSION

NORTHERN BERING SEA

Oceanography and seabird distribution

This study found consistent patterns of densities and distribution of seabirds in the northern Bering Sea, with the pattern usually consisting of densities in Anadyr Water ≥ densities in Bering Shelf Water ≥ densities in Two-layered Water > densities in Alaska Coastal Water. In total density and seven of nine significant cases (Northern Fulmar, Short-tailed Shearwater, Pomarine Jaeger, Black-legged Kittiwake, Common Murre, Least Auklet, and Crested Auklet), the greatest densities and/or frequencies of occurrence were in Anadyr Water. Only Parakeet Auklets and Tufted Puffins were most strongly attracted to water masses other than Anadyr Water and/or Bering Shelf Water. Parakeet Auklets occurred most frequently in Two-layered Water and Alaska Coastal Water, and Tufted Puffins occurred most frequently in Two-layered Water. In the area sampled, the Anadyr Strait area and the area northwest of St. Lawrence Island were the most important areas for feeding by seabirds, probably because of the proximity of these areas to the Anadyr Current.

Patterns of the quantitative distribution of seabirds recorded in this study reflect the quantitative distribution of potential or known prey in this area. The highest biomass of zooplankton in size ranges (4-10 mm) that easily could be taken by seabirds occurs in Anadyr Water (approximately 5 g/m^2 dry weight; Springer *et al.* 1989), followed by Bering Shelf Water and probably by Two-layered Water (i.e., there is some Bering Shelf Water on the bottom); the lowest biomass of "edible" zooplankton occurs in Alaska Coastal Water. In reality, the biomass of total zooplankton in Alaska Coastal Water is

similar to that in Bering Shelf Water (Springer *et al.* 1989), but the additional trophic steps result in energy that is only 25% of that available to seabirds in Anadyr Water (Walsh *et al.* 1989). Little is known about the distribution of fishes in the northern Bering Sea, but schooling species (e.g., arctic cod, Pacific sand lance) appear to occur primarily in Alaska Coastal Water, with some apparently also found near the western shore of St. Lawrence Island, where the biomass of zooplankton is highest; in this location, fishes also are eaten by seabirds (Springer *et al.* 1987). In the southeastern Chukchi Sea, densities of fishes are higher in Alaska Coastal Water than in Bering Shelf and Anadyr waters (Piatt *et al.* 1991).

Although there was a good fit of the general distribution of many seabird species to that of available food, five species did not exhibit clear responses to water masses. Some species probably did not exhibit a response because their densities were too low overall (e.g., Glaucous Gull, Thick-billed Murre, Horned Puffin), because they responded to fronts (e.g., Ancient Murrelet), because they responded to other cues (e.g., Red Phalaropes and gray whales), because they were ecological generalists (e.g., Glaucous Gull), or simply because they may not respond to water masses in general.

Red Phalaropes probably responded to other cues. First, they spent much time following gray whales that feed in the central Chirikov Basin, west of the front. These birds repeatedly altered flight and flew toward gray whales that blew while feeding, sometimes reversing flight directions several times in a few seconds. This positive response to feeding marine mammals was the strongest that I have ever seen at sea. In both the Chirikov Basin (Obst and Hunt 1990, *contra* Harrison 1979) and the eastern Chukchi Sea (F. H. Fay, University of Alaska, Fairbanks, AK, pers. comm.), phalaropes frequently associate with feeding gray whales. In addition to the association with gray whales, Red Phalaropes concentrate near microscale fronts, convergences, and

divergences while feeding. For example, one main feeding area for this species in mid-late summer is in microscale, ephemeral convergent tidal fronts that occur in passes between islands in the Aleutian Islands (Day, pers. obs.). Thus, gross features such as macroscale water masses may not be important to this species in finding food at sea, except in a very general sense.

Some of these species can respond quickly and dramatically to changes in the distribution of some of these water masses. For example, both Bédard (1969) and Springer and Roseneau (1985) found that auklets at western St. Lawrence Island exhibited an ability to respond rapidly to changes in the locations and availability of the "better" feeding areas. Northeasterly winds apparently cause localized upwelling of Anadyr Water off the western coast of St. Lawrence, and auklets breeding on western St. Lawrence Island feed just off the coast during these times, whereas they feed farther offshore, in the main part of the Anadyr Current, during most other times. Further, Hunt *et al.* (1990) found that Least Auklets at St. Lawrence Island overfly unstratified water to forage in stratified water farther offshore, even though both waters contain their preferred prey; they believed that it was easier for the auklets to forage in the stratified water.

The results of this study suggest that Anadyr Water and Bering Shelf Water were "better" for plankton feeders than for fish/nekton feeders; ratios in densities were approximately 7-8 : 1. Conversely, Two-layered Water was "better" for fish/nekton feeders than for plankton feeders; the ratio in densities was approximately 1.5 : 1. Alaska Coastal Water was similar to Two-layered Water, in that birds of both types were able to exploit it; the ratio in densities was approximately 1 : 1. In reality, Anadyr Water had the highest absolute densities of fish/nekton feeders, although these birds represented only 13.6% of the total avifauna in that water mass and only 11.6% of the total avifauna in Bering Shelf Water. In contrast, although their absolute densities were lower than in

Anadyr Water, fish/nekton feeders represented a higher percentage of the total avifauna in Two-layered Water and Alaska Coastal Water (61.8% and 45.8%, respectively). Thus, there appeared to be two main trophic assemblages: a primarily zooplankton-feeding assemblage, with fish/nekton feeders a minor component in Anadyr and Bering Shelf waters, and an assemblage of roughly equal parts of zooplankton feeders and fish/nekton feeders in Two-layered and Alaska Coastal waters.

The results of this study suggest that Anadyr Water and Bering Shelf Water were "better" for diving feeders than for surface feeders; the ratio in densities was approximately 10 : 1. Conversely, Alaska Coastal Water was "better" for surface feeders than for diving feeders; the ratio in densities was approximately 3.3 : 1. Two-layered Water lay somewhere between (the ratio in densities was approximately 1 surface feeder : 1.5 diving feeder), in that surface feeders probably were responding to the presence of Alaska Coastal Water at the surface but some diving feeders also were able to exploit the boundary layer or the Bering Shelf Water lying on the bottom. In other words, diving feeders were not prevented from feeding here because of the upper layer of Alaska Coastal Water. In this context, I believe that it is significant that shallow divers (e.g., Short-tailed Shearwater, Least Auklet) occurred primarily in Anadyr Water and Bering Shelf Water, whereas deep divers (e.g., Parakeet Auklet, Tufted Puffin, Horned Puffin) were able to exploit the Two-layered Water that had deeper, more-productive Bering Shelf Water lying beneath the Alaska Coastal Water (see Figs. 3c and 3d).

Oceanographic fronts and seabirds

The correlation results indicated that a mixture of zooplankton feeders (Short-tailed Shearwaters, Ancient Murrelets, and Least and Crested auklets), fish/nekton feeders (Black-legged Kittiwakes, Common Murres, and Tufted Puffins), and omnivores

(Northern Fulmar, Glaucous Gull) was associated with the front between Bering Shelf Water and Alaska Coastal Water. At the same front in the southeastern Chukchi Sea, Short-tailed Shearwaters, Red Phalaropes, and Least Auklets concentrated in late August 1988 (Piatt *et al.* 1991). Fronts occur as several types and in several scales and tend to be zones of enhanced productivity or zones where potential prey, such as zooplankton, squids, and fishes, tend to become concentrated (Pingree *et al.* 1974, Bowman and Esaias 1978, Owen 1981, Gong *et al.* 1985).

Although the actual dynamics of water movement in fronts are not well understood, Mooers *et al.* (1978) present a model that helps explain the mechanism that concentrates zooplankton in a front. This model suggests that, at least for some types of fronts, there is upwelling on the seaward edge of the front and downwelling on the landward edge. If the rate of vertical advection is high, subsurface zooplankton may be brought to the water's surface on the seaward edge of the front, resulting in an excellent feeding area for surface-feeding birds. If the rate of vertical advection is lower, zooplankton may attempt to maintain their vertical location in the water column; as a result, they may become concentrated in both the upwelling and downwelling portions of the front, resulting in an excellent feeding area for subsurface-feeding birds. Shallow sea fronts are formed in continental seas and occur in boundary regions between shallow wind- and tidally-mixed nearshore waters and stratified offshore waters (Bowman and Esaias 1978). Examples of such fronts include the Middle and Inner fronts on the Bering Sea shelf (Iverson *et al.* 1979, Coachman 1986) and fronts on the North Sea shelf (Pingree *et al.* 1974). Because upwelling may occur at the surface of such fronts, convergence will occur nearby, with a zone of surface scum or flotsam visible from the air (Simpson and Pingree 1978). Bourne and Clark (1984) documented feeding by several species of seabirds along such a frontal line off Valparaiso, Chile. Associations

between seabirds and shallow sea fronts are common (Pingree *et al.* 1974, Schneider 1982, Kinder *et al.* 1983, Haney and McGillivary 1985b, Follestad 1990, Harrison *et al.* 1990, Schneider *et al.* 1990, Piatt *et al.* 1991).

I suspect that some of the other species studied here would have shown significant associations with the front in most cases, if their densities in this area had been higher overall. For example, Northern Fulmars, which were not abundant in this area, are strongly attracted to convergent tidal fronts in passes between the Aleutian Islands (Day, pers. obs.). Similarly, Glaucous Gulls were not abundant anywhere in this area. Off the Oregon coast, however, other gulls such as Western Gulls concentrate in the strong thermal fronts along the edges of the coastal upwelling (Day, pers. obs.). In addition, migrating Red Phalaropes and Red-necked Phalaropes in the South Atlantic Bight concentrate along thermal midshelf fronts (Haney 1985).

In the southeastern Bering Sea, surface-feeding birds such as Northern Fulmars and Fork-tailed Storm-Petrels aggregate significantly near the outer front, whereas diving feeders such as Short-tailed Shearwaters and murres concentrate near the inner front and near a shallow front near the Pribilof Islands (Schneider 1982, Kinder *et al.* 1983). (The inner front in the southeastern Bering Sea is analogous to the front between Bering Shelf Water and Alaska Coastal Water in the northern Bering Sea.) Seabirds aggregated near both the outer and inner fronts, although the species-composition and feeding methods differed between the fronts. Although this study found that auklets aggregated near fronts in the northern Bering Sea, Schneider (1982) and Kinder *et al.* (1983) did not find that auklets aggregated near fronts in the southeastern Bering.

In the southeastern Bering Sea, Short-tailed Shearwaters in particular concentrate along the inner front, where they feed on neritic euphausiids and amphipods, particularly *Thysanoessa raschii* and *Parathemisto libellula*, respectively (Hunt *et al.* 1981a,b). These

species probably are important prey for the zooplankton-feeding seabirds that concentrate along the inner front in the northern Bering Sea. Further, the mid-shelf copepod *C. marshallae* probably concentrates along the western side of this front, in Bering Shelf Water, where it also would be available to diving seabirds. (Springer *et al.* [1989] found such a concentration on the western side of this front in July 1985.) In addition, the upwelling that appears to occur in the center of this front in some areas would make these zooplankters more available to seabirds (see Schneider *et al.* 1990). Finally, the presence of this front in an essentially unbroken line from the southeastern Bering Sea to Pt. Barrow allows a continuous foraging habitat and perhaps a continuous source of orientation for Short-tailed Shearwaters that migrate as far northward as the Beaufort Sea.

The inner front also appears to represent an important feeding zone for some seabirds in the Chukchi Sea. For example, Swartz (1967) found a strong association between murre densities and the thermal front between Bering Shelf Water and Alaska Coastal Water near the entrance to Kotzebue Sound. There, densities of murres decreased abruptly as the ship crossed rapidly from water $< 9^{\circ}C$ to water $> 12^{\circ}C$, while moving eastward from what was probably Bering Shelf Water to Alaska Coastal Water. The importance of this front farther north is unclear, however, as neither murres nor kittiwakes breeding at Cape Thompson and Cape Lisburne are known to concentrate along it (Springer *et al.* 1984, but see Piatt *et al.* 1991). In some parts of the southeastern Chukchi Sea, Parakeet Auklets concentrate along the thermal front, whereas Least Auklets and Parakeet Auklets concentrate along this front in other parts of the Chukchi (Piatt *et al.* 1991). In addition, Harrison *et al.* (1990) found that Northern Fulmars, Red Phalaropes, and Least Auklets concentrated at a front in the Chirikov Basin between Anadyr Water and Bering Shelf Water.

Elsewhere, the importance of thermal fronts to seabirds also has been shown. For example, Cory's Shearwaters in the South Atlantic Bight concentrate near Gulf Stream fronts, and their densities decrease with distance from the front, increase with change in temperature (i.e., near the frontal region of greatest temperature change), and increase with change in fluorescence values (Haney and McGillivary 1985a). In the South Atlantic Bight, Audubon's Shearwaters and Northern Gannets also concentrate near midshelf fronts. When these fronts are present, the shearwaters move inshore from their more common oceanic habitats and the gannets move offshore from their more common nearshore habitats, to feed in the frontal zone (Haney and McGillivary 1985b). Off the coast of Norway, Dovekies concentrate along what appears to be a shelf-break front (Follestad 1990). In the oceanic North Pacific, seabirds of several species, including Cook's Petrels, Juan Fernandez Petrels, and Red Phalaropes, concentrate in the broad Subarctic Frontal zone (this study). Finally, in the Aleutian Islands, Alaska, Whiskered Auklets are specialists that feed in nearshore, convergent tidal fronts (Day and Byrd 1989).

Although salinities are characteristic of differences between water masses in the northern Bering, abrupt changes in salinities along transect lines were not correlated with marked changes in densities of seabirds there. Why the seabirds did not concentrate around the salinity fronts in this area is not entirely clear. Although there have been few studies of those attributes of fronts that concentrate prey, it is possible that temperature is either more important than salinity in concentrating potential prey or an easier environmental cue for seabirds to sense, or both. Temperature is well known as a major factor affecting the distribution of fishes (Lapkin *et al.* 1983). In addition, a marked change in temperature strongly affects metabolism, swimming speed, feeding rates, growth rates, reproduction, and other activities of fishes, whereas a change in salinity

affects only osmoregulation. Indeed, at a front in the southeastern Chukchi Sea, Piatt *et al.* (1991) found that fishes exhibited significant, negative relationships with gradients in sea-surface temperatures but non-significant relationships with sea-surface salinities. In addition, the importance of fishes in the diets of breeding seabirds in the northern Bering and southern Chukchi seas decreases in colder years (Springer *et al.* 1984), indicating that temperatures play a large part in the distribution and abundance or availability of fishes in this cold-water region. Results of this study and those of Pocklington (1979), Schneider (1982), Kinder *et al.* (1983), Abrams (1985), and Haney and McGillivary (1985a,b) suggest that water temperature, rather than salinity, is most important in determining the distribution of seabirds in general, especially around fronts.

NORTHERN NORTH PACIFIC OCEAN

Water masses

As shown by Roden (1972), interannual differences in the broad-scale thermohaline structure of the central North Pacific are small. The stations in the present study indicated that the same water masses were present in about the same locations each year and that the fronts were also, although their exact locations and strengths varied slightly. In addition, sampling in 1984 indicated the presence of the strongly-saline Subtropical Front at 33-31°N and Subtropical Water south of there.

Although the water-column structure generally was similar between years, four primary differences were found. The first difference was that waters of the surface layer were warmer in 1984 than in 1985, particularly in the central and northern part of the Ridge Domain, where they were more than 12°C in 1984 but only a little over 8°C in 1985. The second difference was that waters of the surface layer were less saline in 1984 than in 1985, particularly in Subarctic Water. These two differences may reflect the

generally more stormy and cool weather in this area in 1985, whereas weather in 1984 generally was calm and warm. The third difference was that all water masses shifted slightly northward by approximately one degree of latitude in 1985. Finally, thermal and haline gradients in the Subarctic Front were about 70% as strong in 1985 as they were in 1984.

Biological communities

There were two major zones of zooplankton biomass in each year, a high one north of 40°N and a much lower one south of there. There also was a pattern in both years of higher biomass both to the north and to the south of the center of the Alaska Gyre. This pattern apparently is fairly consistent temporally, for Fager and McGowan (1963) also found the highest densities of the major subarctic zooplankton species to the north and south of the center of this gyre. Apparently, increased winter winds increase the rate of upwelling in the center of the Alaska Gyre, resulting in the lateral advection of zooplankton to the edges of the gyre (Brodeur and Ware 1992).

Although there were two main zones of zooplankton biomass, there are three major zooplankton species-assemblages in this region (Bieri 1959; McGowan 1960, 1971, 1986; Brinton 1962; Fager and McGowan 1963; Briggs 1974). The northernmost assemblage is a "subarctic assemblage," which ranges from Subarctic Water south to northern Transition Domain Water. The second assemblage is a "transitional assemblage," which encompasses Transition Domain Water, the Subarctic Front, and Transition Zone Water; there is some overlap between these two assemblages in northern Transition Domain Water. The third assemblage is a "subtropical assemblage," which ranges south from approximately the Subarctic Front to the southern part of the North Pacific Central Gyre (i.e., to approximately 20°N). There is overlap between this

subtropical assemblage and the transitional assemblage over most of the Transition Zone Water.

Fishes also exhibited three main assemblages in the Central North Pacific. The first was a "subarctic assemblage," which consisted of the salmon species, skilfish, and eight-armed squid and occurred only in Subarctic Water. The second assemblage was a "transitional assemblage," which consisted of smalleye squaretail, Pacific saury, and albacore (plus, to some extent, Pacific pomfret) and could be compared with the transitional assemblage of zooplankton. These species occurred from southern Subarctic Water to the Subarctic Front and, occasionally, south of it. It is unclear why many of these species have such extensive ranges, but it may be related to the fact that these transitional conditions are extensive latitudinally in this part of the northern North Pacific. The final assemblage was a "subtropical assemblage," which consisted of the blue shark, neon flying squid, skipjack and bigeye tunas, billfishes, and flying fishes. All are warm-water species that ranged northward to the Subarctic Front and sometimes to the north of it. The importance of warm sea-surface temperatures to these warm-water species is suggested by their more-southerly distributions during the cooler summer of 1985. No sampling was conducted in the vicinity of the Hawaiian Islands, where there may be a truly tropical assemblage (Briggs 1974).

Three major assemblages of seabirds were indicated by this study. The first was a "subarctic assemblage," which occurred at the highest densities of all assemblages. It consisted of the highest densities of Northern Fulmars, Sooty, Short-tailed, and Buller's shearwaters, Mottled Petrels (and, to a great extent, Solander's Petrels), Fork-tailed Storm-Petrels (and, in 1985, Leach's Storm-Petrels), Black-legged Kittiwakes, alcids (i.e., murres and puffins), and most jaegers and skuas. Some of the jaegers occurred in other water masses, but they tended to congregate around concentrations of other

seabirds, which were most abundant in Subarctic Water. Nine (56.3%) of the 16 taxa considered to be subarctic exhibited primarily a water mass effect, none (0%) exhibited primarily a year effect, and only one (6.3%) exhibited primarily a water mass-year interaction.

The second assemblage consisted of species that were restricted to the vicinity of the Subarctic Front, using primarily the front and transitional waters on either side of the front. This "transitional assemblage," which had the second-highest densities of all assemblages, consisted of the highest densities of Juan Fernandez and Cook's petrels, Leach's (particularly in 1984), Band-rumped, and Sooty storm-petrels, and Red Phalaropes. Although information on foods used by these species in this remote part of the northern Pacific Ocean is nonexistent, most or all of them are surface-feeding seabirds that feed primarily on zooplankton and small fishes and squids. The Subarctic Front is an area of hydrostatic instability (Roden 1970, 1972), which should make it an excellent feeding area for seabirds of this type. Indeed, microscale, ephemeral convergence and divergence zones were scattered at the surface throughout this region, and these birds occasionally were seen feeding in them (Day, pers. obs.). In the eastern tropical Pacific, Leach's Storm-Petrels may feed diurnally on mesopelagic fishes that are feeding at the surface or are raised to the surface by microscale upwellings (Pitman and Ballance 1990). Four (66.7%) of the six taxa considered to be transitional exhibited primarily a water mass effect, none (0%) exhibited primarily a year effect, and only one (16.7%) exhibited primarily a water mass-year interaction.

The third assemblage consisted of species that were restricted to warm, high-salinity water, from the Subarctic Front (occasionally) to Subtropical Water. This "subtropical/tropical assemblage" occurred in the lowest densities of all assemblages: except in waters immediately off the Hawaiian Islands, densities rarely exceeded 0.1

bird/km^2. This assemblage consisted of the highest densities of Bulwer's, Dark-rumped, and Herald petrels, Wedge-tailed and Newell's shearwaters, Red-tailed and White-tailed tropicbirds, Red-footed Boobies, Sooty Terns, and Brown Noddies. These species are subtropical to tropical in distribution, with some (e.g., Sooty Tern) being pantropical in distribution (Harrison 1983). None (0%) of the three taxa considered to be subtropical/tropical exhibited primarily a water mass effect, one (33.3%) exhibited primarily a year effect, and none (0%) exhibited primarily a water mass-year interaction. Another seven species were seen only in this habitat (and clearly are subtropical or tropical), but I was unable to examine their distributions with a two-way ANOVA. Although few of these species exhibited statistically-significant relationships with water masses, all occurred in densities and frequencies that were so low overall that the statistical tests were unable to detect differences. This pattern of very low densities and frequencies apparently is common for seabirds throughout these warmer waters (Gould 1983), and further research may require the development of new analytical techniques to deal with the large number of zeroes that are present in such a data set.

The two albatrosses did not fit into any of the three seabird assemblages, but instead were wide-ranging species in the cool and windy northern North Pacific. Both Laysan and Black-footed albatrosses are generalists in food habits (Harrison *et al.* 1983), which may explain their wide at-sea distributions. In addition, albatrosses in general cover great distances while foraging at sea; individual Wandering Albatrosses in the Subantarctic have been found to cover 3,600-15,000 km in a single foraging trip from their nest (Jouventin and Weimerskirch 1990). The absence of both Laysan and Black-footed albatrosses from the "Subtropical/tropical assemblage" is surprising, because the leeward Hawaiian Islands are their primary breeding grounds. These two species of North Pacific albatrosses apparently were overflying the warmer waters where

they breed to forage extensively over cooler, more-productive waters. A similar pattern was seen by Dixon and Starrett (1952), who observed only 53 albatrosses at sea during 170 h of observation in subtropical and tropical waters between Hawaii, Japan, and the Philippines. Strong winds are important to albatrosses elsewhere (Abrams 1985, Jouventin and Weimerskirch 1990), and the absence of strong winds in Subtropical and Transition Zone waters (Roden 1970) may be the primary factor limiting the distribution of albatrosses there.

In addition to the above patterns, several other species-specific patterns were of interest. For example, several pairs of closely-related species exhibited distributional patterns that suggested avoidance of competition at sea. In Subarctic Water, the two large *Puffinus* shearwaters (Sooty and Short-tailed) exhibited geographic segregation, with Short-tailed Shearwaters concentrating over the Ridge Domain and Sooty Shearwaters concentrating over the Subarctic Current System. Two species of *Pterodroma* petrels exhibited a similar pattern, with Mottled Petrels concentrating over the Ridge Domain and Solander's Petrels concentrating over the Subarctic Current System (and, occasionally, farther south). In addition, two species of *Pterodroma* petrels concentrated in the Subarctic Front, but they may be separated ecologically by size, with Juan Fernandez Petrels being the largest gadfly petrel in the North Pacific and Cook's Petrels being the smallest (Harrison 1983). Finally, the two storm-petrels that breed on the Alaska coast appear to segregate geographically, with Fork-tailed Storm-Petrels foraging primarily within a few hundred miles of the coast and Leach's Storm-Petrels apparently foraging farther offshore, all the way to the Subarctic Front. Such patterns suggest possible directions for further research.

The assemblages discussed here (subarctic, transitional, and subtropical/tropical) suggest that a geographically-stable set of biological communities is present in the

northern North Pacific Ocean. These assemblages are related to well-defined, persistent physical environments. Presumably, the geographic stability of both water masses and lower trophic levels (i.e., prey) is what allows the seabird communities to be stable as well. This suggestion can only be inferred from the data presented here, however, and can not be proven by them. Proof would require a parallel study of seabird trophics along with the collection of at-sea data.

Oceanography and seabird distribution

In many aspects, the distribution of seabirds reflected the distribution of certain physical and biological oceanographic variables. Physical characteristics were used to stratify objectively the area sampled into unique water masses. These water masses appeared to reflect distributions of most of the seabird species. One of the best reflections of the power of this technique is the fact that 14 (82.4%) of the 17 taxa with significant two-way ANOVAs exhibited primarily a water mass effect. Only Bulwer's Petrel (1 species; 5.9%) exhibited primarily a year effect, and only Parasitic Jaeger and Leach's Storm-Petrel (2 species; 11.7%) exhibited primarily a water mass-year interaction (i.e., a change in habitat use between years).

Another aspect of the relationship to oceanography is that of availability of food. Although the zooplankton were not identified to species, the general pattern was of high biomass in Subarctic Water and Transition Domain Water and much lower biomass from the Subarctic Front to Subtropical Water. This pattern of distribution of zooplankton was matched by total densities of seabirds for Subarctic Water in both years, for Transition Domain Water in neither year, for the Subarctic Front in neither year, for Transition Zone Water in both years, and for waters south of there in the one year that they were sampled. In other words, birds in a general sense occur at sea where the food occurs (i.e.,

Subarctic Water) and do not occur where it is not present (i.e., Transition Zone and Subtropical waters). One confusing point, however, is the lack in both years of a correspondence between the biomass of zooplankton in Transition Domain Water and the Subarctic Front and densities of seabirds seen there. Based on the biomass of zooplankton in these water masses, densities of seabirds in Transition Domain Water should have been high and in the Subarctic Front should have been low and similar to those in Transition Zone Water and water masses farther south. Instead, the reverse was true, particularly in 1984. Perhaps the large standing stocks of zooplankton occurred below the strong thermocline and were unavailable to the surface-feeding seabirds that predominate in Transition Domain Water. Densities of seabirds, particularly those feeding near the surface, were higher around the Subarctic Front (particularly in 1984), where hydrodynamic instabilities bring small prey to the surface and microscale convergences apparently concentrate the prey once they are brought there. In contrast, both Transition Zone Water and Subtropical Water south of there apparently have both low densities of zooplankton and little upwelling to bring them to the surface (i.e., there are few vertically-advective structures). Further, most of the zooplankton collected in this area in surface layers were extremely small ($\leq$ 1 mm; Day, pers. obs.), making it difficult for most species of seabirds to forage effectively on zooplankton there.

Although seabirds generally occurred in high densities in areas with high biomass of zooplankton, there was a mesoscale lack of correspondence in the center of the Ridge Domain. In this region, the biomass of zooplankton was much lower than it was around the outer edges of the gyre (Fig. 15), yet the total density of seabirds here was the highest seen anywhere in the entire transect line (Figs. 17 and 18). Reasons for this lack of correspondence are unclear but may be related to the fact that seabirds in general have not been found in exact locations where prey densities are highest (e.g., Woodby 1984, Obst

1985). Hunt (1990) has found that studies of concordance between seabirds and their prey have yielded mixed results; he also has found that concordance is higher in piscivorous seabirds than in planktivorous ones. My interpretation of these results is that the seabirds were attracted to an area with upwelling, which is an area where prey should concentrate, but that the upwelling may not have occurred for a long enough period of time for prey to become concentrated or may not have been strong enough for prey to become concentrated.

There also was a general correspondence between densities of seabirds and CPUEs of fishes and squids, although few of the species and/or size classes examined in this study were eaten directly by seabirds (e.g., Pacific saury). The high CPUEs of fishes and squids in Subarctic Water are indicative of the high availability of prey there for seabirds as well as for fishes and squids. A second concentration of fishes and squids around the Subarctic Front attests to the high availability there, as well, of prey to upper-trophic-level predators. In contrast, fishes and squids were less abundant and were patchy in Transition Zone Water. Although data on biomass were not collected for all species, my impression was that the pattern of biomass of fishes and squids was: Subarctic Water > Subarctic Front > or ≈ Transition Domain Water > Transition Zone Water.

The Subarctic Front appears to be an important feeding area for some species of seabirds, particularly those feeding at the surface (e.g., Leach's, Band-rumped, and Sooty storm-petrels, Juan Fernandez and Cook's petrels, Red Phalaropes). As discussed above, the concentrating mechanism appears to be the fact that prey are both made available and are concentrated at the surface (Owen 1981). Fronts have been shown to be important concentrating mechanisms for seabirds (e.g., Ainley and Jacobs 1981; Schneider 1982; Kinder *et al.* 1983; Abrams 1985; Haney 1985; Haney and McGillivary

1985a,b). In most of these examples, the closest associations were found with thermal fronts, although it is conceivable that the thermal signal was correlated with another variable that the seabirds actually were using. Although the Subarctic Front in general is an area where seabird densities are higher than are those on either side of it (Day, unpubl. data), the frontal zone studied here generally had lower densities of seabirds than were seen farther west (Day, unpubl. data). This difference probably reflects differences in frontal strength and in the strength of the thermal signal. The Emperor Seamounts apparently play a major part in breaking down the strength of the Subarctic Front, with a strong thermal front west of the seamounts but a smaller thermal front east of them (Roden *et al.* 1982).

Ogi (1984) suggested that the northward migration of Sooty Shearwaters in the northwestern North Pacific corresponded with the northward migration of their preferred prey (Pacific saury) as water temperatures increased during the summer. His data suggested that both species responded to increases in sea-surface temperatures, with the shearwaters moving northward slightly in advance of the movements of saury. Data presented here from the central North Pacific suggest that this relationship may not be as strong as suggested by Ogi for the northwestern North Pacific. In 1984, densities of Sooty Shearwaters in Subarctic Water did peak at about one degree of latitude north of one of the peaks of saury CPUEs, but Sooty Shearwaters were not recorded around the second peak of saury CPUEs, which was near the Subarctic Front. Further, CPUEs of saury in 1985 were considerably lower in all areas than in 1984, perhaps because of lower sea-surface temperatures in 1985, whereas densities of Sooty Shearwaters increased by a factor of about five that year. The peak of densities of Sooty Shearwaters occurred in the same latitudinal block in both years, regardless of the distribution and

CPUEs of saury, suggesting that other factors may be causing Sooty Shearwaters to concentrate in the Subarctic Current System at this time of the year.

Comparisons with other studies

The primary research on the distribution of seabirds in the northern North Pacific Ocean has been done by Gould (1983), who collected data between Alaska and Hawaii along 158°W in the fall of 1976, and by Wahl *et al.* (1989), who described assemblages of seabirds in the North Pacific and Bering Sea between 1975 and 1984. Several of the species examined by Gould (1983) had distributions similar to those seen in this study. For example, Sooty and Short-tailed shearwaters, Northern Fulmars, Black-legged Kittiwakes, Mottled Petrels, Horned and Tufted puffins, and Pomarine and Parasitic jaegers were found primarily or exclusively in Subarctic Water; the shearwaters also were found from Transition Zone Water to Subtropical Water, probably while migrating back to breeding grounds in the Southern Hemisphere (Guzman 1981). Further, Red Phalaropes and Leach's Storm-Petrels concentrated around the Subarctic Front in both studies. (Leach's Storm-Petrels also concentrated in the northern Gulf of Alaska but probably were feeding late-fledging chicks.) There also was a large suite of subtropical/tropical birds found from Transition Zone Water to Subtropical water: Red-tailed and White-tailed tropicbirds, Herald and Dark-rumped petrels, and Wedge-tailed Shearwaters. In addition, several other subtropical/tropical species occasionally seen in these water masses were recorded: Kermadec, Bonin, Phoenix, and Black-winged petrels. Two species that I found in the Subarctic Front (Cook's Petrel and Juan Fernandez Petrel [incorrectly called White-wing Petrel on Fig. 3 of Gould (1983); Gould, pers. comm.]) were recorded south of this front, perhaps while migrating to the Southern Hemisphere for breeding. Again, only the two species of albatrosses exhibited

any lack of specialization in at-sea distribution; in fact, they occurred extensively throughout all water masses. The reasons for this distribution are unclear. The albatrosses that I found in Transition Zone Water and Subtropical Water may have been returning to feed young at their breeding colonies in the leeward Hawaiian Islands (Richardson 1957, King 1970).

Wahl *et al.* (1989) described four main assemblages of seabirds in the North Pacific and Bering Sea, two of which occurred in the region discussed in this study. A "Low-Moderate Temperature/Moderate Salinity assemblage" occurred throughout the Subarctic and Transitional Domain water masses, and a "High Temperature/High Salinity assemblage" occurred south of the Subarctic Front. These two assemblages of Wahl *et al.* (1989) correspond to the "subarctic assemblage" and the "subtropical/tropical assemblage," respectively, of this study. Surprisingly, however, they did not detect any species that occurred primarily in and around the Subarctic Front (the "transitional assemblage" of this study). It appears, however, that Wahl *et al.* (1989) considered the Subarctic Front to be nothing more than a line with no width, rather than a narrow (in the western Pacific) to broad (in the central and eastern Pacific) frontal zone. In addition, the data set analyzed by Wahl *et al.* (1989) was more extensive temporally than the July data set examined here, possibly resulting in birds that breed in the Southern Hemisphere being recorded migrating over water masses where they do not feed (e.g., Sooty and Short-tailed shearwaters overflying subtropical and tropical waters to their subantarctic breeding grounds; Guzman 1981).

Another factor possibly obscuring the relationship between distributions of seabirds and the Subarctic Front is the fact that the physical boundaries upon which biogeographic boundaries in the ocean are based often are not very sharp (Backus 1986, Olson 1986). For example, several species of subtropical fishes and squids cross the

Subarctic Front in mid- and late summer, when waters of the Transition Domain and even southern Subarctic Water warm sufficiently. This summer migration enables them to feed in the more productive water north of the Subarctic Front and to spawn south of it (Mishima 1981, Murakami *et al.* 1981). Further, different organisms respond differently to changes in physical variables (Backus 1986). For example, plankton and pelagic nekton occurring in the vicinity of the Subarctic Front include some taxa from more subarctic regions, some from more subtropical and tropical regions, and some endemic species (e.g., see Briggs 1974). Evidence of the uniqueness of this region is found in the large number of endemics other than seabirds that are found here (e.g., Bieri 1959, Brinton 1962, McGowan 1971, Olson 1986), and it is not unreasonable to hypothesize that some species of birds became specialized to feed and live here at some stages of their life cycle.

SOURCES OF ERROR

Several factors may have contributed to errors in this study or may have obscured relationships between seabirds and their environment. These sources fall under three categories: those endemic to both sampling areas and those endemic to one or the other of the two areas.

At least three sources of error are applicable to both studies. First, I was able to collect few data on availability and types of prey in the water column while I was sampling for birds. Further, I had no stomachs of birds collected in the two study areas and, hence, was unable to prove that the conjectured relationships actually did exist. In addition, the accuracy of strip-transect sampling may be compromised by daily or interannual variations in sightability of birds: because of covariation between observation conditions and sightability, periods of poor weather may result in lower estimates of

density than would be generated otherwise. It is doubtful, however, that such a bias occurred consistently enough in this study to compromise the results. Three lines of evidence suggest that such a bias was minimal. First, if observation conditions become so poor that I believe I am missing birds, I simply stop sampling: collecting data of no quantitative value is of questionable value. Second, stormier weather (with accompanying poorer observation conditions) occurred in the more-northerly part of the North Pacific in both 1984 and 1985, yet the lowest densities of birds in both years occurred in more-southerly waters, where observation conditions generally were excellent. Finally, such a bias should affect smaller birds disproportionally, because they are harder to see under poorer observation conditions; however, densities of Leach's Storm-Petrels were higher in the stormier parts of the northern North Pacific in 1985, whereas they should have occurred in higher densities in more-southerly waters. Similar scenarios of biases in the northern Bering Sea can be constructed, but none are plausible.

In the northern Bering Sea, at least two factors may have compromised this study. First, the data were collected over a short period of time in one fall, possibly resulting in patterns that are not applicable to this region in general. Work by Haney (1991) and Piatt *et al.* (1991), however, suggests that similar patterns may occur in the northern Bering Sea in mid-summer and in the southeastern Chukchi Sea in late summer, respectively. In addition, collection of data on acoustically-determined biomass of fishes and zooplankton during the frontal crossings would have helped elucidate reasons for some of the patterns in distribution that I saw.

In the northern North Pacific, one factor may have compromised this study. Although there was some overlap in timing of the two cruises, the 1985 cruise occurred, in general, about 13 days earlier than did the 1984 cruise. Although such a difference in timing seems small, it would result in a difference in sea-surface temperature of about 1°C

between years. As mentioned earlier, however, sea-surface temperatures were up to 4°C colder in 1985 than in 1984, suggesting that other factors resulted in changes in both the physical environment and the biological environment in 1985.

HOW DO SEABIRDS FIND FOOD AT SEA?

I believe that we now can speculate about the main features of the ways in which seabirds find food at sea. It appears that the cues used by the seabird are determined by the scale of the environmental features that the seabird has available to it and by the feeding method and prey type of the seabird. The primary features used apparently are the water mass and winds, which are macroscale features in most cases. After a seabird locates the appropriate water mass, it keys in on one or several meso- or microscale cues that may be important in locating prey or may be correlated with the abundance of prey. These cues are not equally important to all seabirds, however.

The primary feature used for finding food is the water mass. This study and others (e.g., Murphy 1936, Wahl *et al.* 1989, Piatt *et al.* 1991) have shown that many seabirds orient to specific water masses. On the other hand, few, if any, species occur in only one water mass; instead, most occur in several water masses (Ainley and Boekelheide 1983, Wahl *et al.* 1989; this study), probably because physical boundaries in the ocean often are not sharp (Backus 1986, Olson 1986).

Wind may affect the distribution of seabirds in a macroscale sense through its effect on flight capabilities. For example, only in the tropics is the air hot enough to rise, thus allowing the presence of soaring birds (frigatebirds; Ainley and Boekelheide 1983). In most cases, however, seabird species that are believed to be constrained by winds are believed to be constrained by the absence of winds of high speeds. For example, species that have moderate-high wing loadings and aspect ratios and that forage while dynamic

soaring (e.g., albatrosses, large gadfly petrels, *Procellaria* and *Puffinus* shearwaters) are limited in distribution by the presence of pack ice, which inhibits the development of winds for dynamic soaring and which has little open water that can be used for taking off after feeding. In contrast, smaller procellariiform birds that have low wing loadings and aspect ratios (e.g., Antarctic and Snow petrels, prions) depend more on flapping flight than on dynamic soaring and, hence, can forage within the pack ice (Griffiths 1983, Fraser and Ainley 1986). Other examples of the use of winds for foraging and in limiting foraging include albatrosses in the North Pacific (this study) and the Subantarctic (Jouventin and Weimerskirch 1990) and Sooty Terns in the Indian Ocean (Ainley and Boekelheide 1983). In this context, it may be significant that the primary seabirds occurring in Transition Zone and northern Subtropical waters of the northern North Pacific, where wind stress is minimal (Roden 1970), were smaller species with low wing loadings (e.g., gadfly petrels, Bulwer's Petrels, storm-petrels).

Although many seabirds first locate the appropriate water mass, it is clear that densities of a particular species are not uniform within a water mass (e.g., this study). These variations in within-habitat densities suggest that meso- to microscale cues are used within particular water masses (Hunt 1990). These smaller-scale cues include both mesoscale variables such as oceanographic fronts and zones of coastal upwelling and microscale variables such as small physical structures that are visible from above the ocean (e.g., internal waves, Langmuir cells), structure of the water column, winds, marine fishes and mammals, other seabirds, and possibly aerosols.

Oceanographic fronts are meso- to microscale structures that clearly are important to seabirds. Fronts are zones of rapid change in one or more oceanographic variables (e.g., sea-surface temperature or salinity, water color, density) and represent boundaries between water masses of different histories (Bowman and Esaias 1978). Further, they

occur as several types and in several scales and tend to be zones of enhanced productivity or zones where prey tend to become concentrated (Bowman and Esaias 1978). Of the six main types of fronts, shallow sea fronts, shelf-break fronts, convergent fronts, and divergent fronts are of major interest to seabirds. Shallow sea fronts are formed in continental seas and occur in boundary regions between shallow wind- and tidally-mixed nearshore waters and stratified offshore waters (Bowman and Esaias 1978). Because upwelling may occur at the surface of these fronts, convergence will occur nearby, with a zone of surface scum or flotsam visible from above the ocean (Simpson and Pingree 1978). Such fronts are highly important to seabirds (Pingree *et al.* 1974, Schneider 1982, Kinder *et al.* 1983, Bourne and Clark 1984, Haney and McGillivary 1985b, Follestad 1990, Harrison *et al.* 1990, Schneider *et al.* 1990, Piatt *et al.* 1991). Shelf-break fronts, which are formed at the boundary between shelf and slope waters (Bowman and Esaias 1978), also are important to seabirds (Brown *et al.* 1975, Rowlett 1980, Schneider 1982, Ainley *et al.* 1984, Haney and McGillivary 1985a, Veit 1985). Convergent fronts primarily are boundary current fronts, where two currents meet and the denser current flows under the lighter one (Bowman and Esaias 1978, Brown 1980). Such fronts are moderately important to seabirds (Jehl 1974, Brown 1980, Rowlett 1980, Briggs *et al.* 1984, Haney 1985). Divergent fronts are upwelling fronts; they essentially are the surface manifestation of an inclined pycnocline, with the isopycnal water able to be mixed deeply by winds (Bowman and Esaias 1978). Associations between seabirds and divergent fronts have been found by Brown (1979), Briggs *et al.* (1984), and Briggs and Chu (1986).

Coastal upwelling is another mesoscale variable that is stable both geographically and temporally and appears to be important to seabirds. Caused by offshore movement of surface waters that results from the along-shore flow of winds, coastal upwelling

results in high productivity in a fairly narrow zone along the coast (Bowman and Esaias 1978). These zones of coastal upwelling include the coastal upwelling system off western North America (Briggs *et al.* 1984, 1987), the Peruvian upwelling system off western South America (Murphy 1925, 1936), the Senegal upwelling off northwestern Africa (Brown 1979), the Benguela upwelling off southwestern Africa (Summerhayes *et al.* 1974, Burger and Cooper 1984), and the Arabian upwelling (Bailey 1966). Smaller versions of coastal upwelling also may occur: off a sand spit at Teller, Alaska, in September 1985, I observed small-scale coastal upwelling that was driven by nearly-along-shore winds of approximately 40 kt. The surface water at the lee side of the spit appeared to be driven offshore, resulting in a small (approximately 50 m wide) zone of upwelling with a small line of white foam at the outer edge. Glaucous Gulls and Black-legged Kittiwakes fed at the surface in the upwelling zone, and Pelagic Cormorants fed by diving just inshore of the white foam.

Microscale physical structures that are visible from the air include both internal waves and Langmuir cells; both appear to be used by seabirds. Internal waves are subsurface waves that occur between waters of different density and that exhibit near-microscale manifestations at the surface of the ocean when wind speeds are less than 15 kt (Haney 1987). They are caused by flow of a current through narrow passes or over areas of irregular bathymetry and are exhibited at the ocean's surface by long, parallel slicks (wave troughs or downwelling) and zones of rough water (wave crests or upwelling). Haney (1987), the only author to investigate such structures, found that several species of seabirds concentrated at the crests of internal waves in the western North Atlantic. Internal waves probably are detected visually by birds flying above the ocean, for the alternating bands of calm and rough water are evident even to an observer on a ship. Langmuir cells are microscale, surface circulation cells that are caused by

moderate winds blowing at uniform speeds and result in a series of long lines of calm, convergent water (downwelling) alternating with long lines of upwelling (Brown 1980). The importance of Langmuir cells to seabirds has been studied little, but phalaropes, small gulls, and terns have been found feeding in the convergence lines of such cells off Peru (Brown 1980).

The importance of microscale structure of the water-column to seabirds is still being evaluated, but the picture that is emerging suggests that it is important to subsurface-foraging seabirds such as alcids. Briggs *et al.* (1987) first suggested that structure of the water-column may affect the at-sea distribution of diving seabirds. The hypothesis suggests that diving seabirds should select to forage in areas where the pycnocline is shallow (because it will require less energy to dive a few meters below the water's surface than it will to dive tens of meters below it) and where the pycnocline is weak (because strong pycnoclines are associated with subsurface shear, which would increase the amount of energy expended while foraging). Hunt *et al.* (1990) and Haney (1991) examined this hypothesis in the same area of the northern Bering Sea and found somewhat conflicting results. For example, Hunt *et al.* (1990) found that Least Auklets occurred in highest densities where the thermocline was strong (i.e., in stratified water), whereas Haney (1991) found that they generally avoided stratified water and instead concentrated in vertically-mixed water. Both studies, however, found that densities of Least Auklets in stratified water were higher in areas where the upper layer was shallow; such a preference is consistent with a need for this small seabird to forage at shallow depths to save energy. In the same area, 79% of all murres, 94% of all Parakeet Auklets, and 96% of all Crested Auklets occurred over stratified water, again suggesting that structure of the water column may be important (Haney 1991).

Marine fishes and mammals represent a form of microscale patchiness to seabirds, with the primary method of detection of foraging activity of marine fishes and mammals being visual. The response appears to be related to feeding or expectations of feeding and involves one or more forms of commensalism between the seabirds and the marine fishes and mammals. Predation on schooling fishes by predatory marine fishes results in escape behavior that is accompanied by the prey fishes' jumping out of the water or splashing at the surface and, thus, becoming available to seabirds (Colblentz 1985, Au and Pittman 1988). Predation or simple swimming movements of marine mammals may make feces available to some seabirds (Routh 1949, Ryder 1957, Williams *et al.* 1990), may increase the availability of zooplankton to some seabirds (Ryder 1957, Harrison 1979), may move some prey upward in the water column to a location where they can be preyed upon by seabirds (Routh 1949, Harrison 1979, Evans 1982, Pierotti 1988, Obst and Hunt 1990), may make food scraps available to seabirds (Evans 1982, Williams *et al.* 1990), or may lead seabirds to food (Routh 1949; Au and Pittman 1986, 1988).

Other seabirds also may be used as microscale cues for determining where to forage (Hoffman *et al.* 1981): "If other birds are successful at finding food here, I should try here also." In Alaska, some species (e.g., Sooty and Short-tailed shearwaters, *Larus* gulls, Black-legged Kittiwakes) are catalysts for the formation of feeding flocks, whereas others (e.g., shearwaters) interfere with the ability of other species to feed and disperse prey, thus shortening the time that a flock may feed. Diving species are able to determine if kittiwakes are feeding on single fishes or schools of fishes and approach only the latter (Hoffman *et al.* 1981).

The olfactory abilities of procellariiform seabirds (Hutchinson and Wenzel 1980, Hutchinson *et al.* 1984) suggests that aerosols over certain waters could be attractive to these seabirds. Although this cue may not be available to all seabirds, some species

certainly use it. For example, I have seen Northern Fulmars travel several kilometers from the nearest known at-sea range when attracted to a large amount of blood and scraps that was put into the water during cleaning of fishes; this attraction occurred during a period of heavy sea fog, when the birds could not have seen the fish offal being put into the water.

SUMMARY AND CONCLUSIONS

In the northern Bering Sea, densities of seabirds in Anadyr Water and the Bering Shelf Water were very high, with peak densities of several hundred birds/km^2; densities of seabirds in the less-productive Two-layered Water and Alaska Coastal Water were much lower. Anadyr Water and Bering Shelf Water both are highly productive and contain a high biomass of zooplankton in a size that easily can be eaten by seabirds. In contrast, Alaska Coastal Water contains a lower biomass of zooplankton in general and primarily small zooplankters that are food for fishes but mostly are too small for direct consumption by seabirds. This water mass seems to be "better" for piscivorous seabirds than for planktivorous ones (also see Piatt *et al.* 1991).

In the northern North Pacific, overall densities of seabirds were much higher in Subarctic Water and Transition Domain Water than in Transition Zone Water, the Subtropical Front, and Subtropical Water; densities in the Subarctic Front were high in one year but low in the other. These differences were consistent with the much higher biomass of zooplankton and higher CPUEs of fishes and squids in the Subarctic and Transition Domain water masses than in the more subtropical ones. The lack of interannual consistency in the density of seabirds in the Subarctic Front is confusing, for there was a high biomass of zooplankton and high CPUEs of fishes and squids there in both years. Hydrostatic instabilities in this front, however, actually may make the food that is present highly available to seabirds.

The data presented here indicate that many species of seabirds in the northern Bering Sea and northern North Pacific Ocean exhibited clear relationships to macroscale oceanographic features. Further, the data for the northern North Pacific clearly indicate

that these patterns are repeatable interannually and that some interannual variations in distributions of seabirds reflect interannual variations in oceanography. Finally, the data indicate that some mesoscale variables also are important in affecting the distribution of some seabirds; mesoscale fronts in the Bering Sea fall into this category.

A few species of seabirds did not exhibit clear relationships to macroscale oceanographic features. In some cases, this lack of relationship was due to insufficient numbers or insufficient frequencies to enable a pattern to be exhibited statistically (e.g., Glaucous Gull in the northern Bering Sea, Sooty Storm-Petrel and Herald Petrel in the northern North Pacific). Other exceptional species appeared to have been responding to mesoscale or microscale characteristics (e.g., microscale convergence lines embedded within the large Subarctic Front of the North Pacific), and some may have been orienting to other variables (e.g., the relationship of Red Phalaropes with gray whales in the Bering Sea, the relationship of albatrosses with winds in the northern North Pacific).

In conclusion, the ways in which seabirds forage at sea are complex and probably are organized hierarchically. The first level of selection for foraging certainly must be the macroscale variable (i.e., water masses, winds). Below that level, however, it is unclear whether there are other levels of hierarchy or if all of the meso- and microscale variables are equally important. Mesoscale variables that are geographically and/or temporally stable probably are more important than are microscale cues, which often are geographically and/or temporally ephemeral and certainly are difficult to locate. For example, it probably is easier to locate zones of coastal upwelling or large frontal zones at sea than it is to locate ephemeral, internal waves or microscale convergences within fronts. Hence, mesoscale variables probably are the second level used for orientation. Finally, microscale cues such as microscale convergences, internal waves, and Langmuir cells probably are the lowest or finest level of hierarchy that a seabird uses in determining

where to forage. The availability of such cues does not, however, mean that they are needed or used by all seabirds. For example, I earlier presented examples of species that did not exhibit identifiable responses to the environment. In addition, winds necessary for dynamic soaring probably are not important to diving seabirds, a knowledge of microscale structure of the water column probably is not important to or measurable by a surface-feeding seabird, and aerosols probably are not important to seabirds that forage visually and cannot smell them. Both interspecific differences in physical characteristics of seabirds and heterogeneity of the marine environment result in a suite of responses that certainly vary among species within one area and probably vary within one species among different areas.

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APPENDIX 1. COMMON AND SCIENTIFIC NAMES OF INVERTEBRATES, ELASMOBRANCHS, FISHES, BIRDS, AND MAMMALS MENTIONED IN TEXT.

Common name	Scientific name
INVERTEBRATES	
Eight-armed squid	*Gonatopsis borealis*
Boreal clubhook squid	*Onychoteuthis borealijaponica*
Neon flying squid	*Ommastrephes bartrami*
ELASMOBRANCHS[1]	
Blue shark	*Prionace glauca*
FISHES[1]	
Sockeye salmon	*Oncorhynchus nerka*
Chum salmon	*Oncorhynchus keta*
Pink salmon	*Oncorhynchus gorbuscha*
Coho salmon	*Oncorhynchus kisutch*
Chinook salmon	*Oncorhynchus tshawytscha*
Steelhead	*Oncorhynchus mykiss*
Total salmon	*Oncorhynchus* spp.
Arctic cod	*Boreogadus saida*
Pacific saury	*Cololabis saira*
Total billfishes	*Tetrapturus* spp.
Pacific pomfret	*Brama japonica*
Pacific sand lance	*Ammodytes hexapterus*
Skipjack tuna	*Euthynnus pelamis*
Albacore	*Thunnus alalunga*
Bigeye tuna	*Thunnus obesus*
Smalleye squaretail	*Tetragonurus cuvieri*
Skilfish	*Erilepis zonifer*
Total flying fishes	Exocoetidae
BIRDS[2]	
Red-throated Loon	*Gavia stellata*
Pacific Loon	*Gavia pacifica*
Common Loon	*Gavia immer*
Wandering Albatross	*Diomedea exulans*
Black-footed Albatross	*Diomedea nigripes*
Laysan Albatross	*Diomedea immutabilis*
Northern Fulmar	*Fulmarus glacialis*
Antarctic Petrel	*Thalassoica antarctica*
Snow Petrel	*Pagodroma nivea*

APPENDIX 1. COMMON AND SCIENTIFIC NAMES OF INVERTEBRATES, ELASMOBRANCHS, FISHES, BIRDS, AND MAMMALS MENTIONED IN TEXT (CONTINUED).

Common name	Scientific name
BIRDS (CONTINUED)	
Dark-rumped Petrel	*Pterodroma phaeopygia*
Juan Fernandez Petrel	*Pterodroma externa*
Phoenix Petrel	*Pterodroma alba*
Mottled Petrel	*Pterodroma inexpectata*
Solander's Petrel	*Pterodroma solandri*
Kermadec Petrel	*Pterodroma neglecta*
Herald Petrel	*Pterodroma arminjoniana*
Cook's Petrel	*Pterodroma cookii*
Bonin Petrel	*Pterodroma hypoleuca*
Black-winged Petrel	*Pterodroma nigripennis*
Gadfly petrel	*Pterodroma* spp.
Bulwer's Petrel	*Bulweria bulwerii*
Cory's Shearwater	*Calonectris diomedea*
Wedge-tailed Shearwater	*Puffinus pacificus*
Buller's Shearwater	*Puffinus bulleri*
Sooty Shearwater	*Puffinus griseus*
Short-tailed Shearwater	*Puffinus tenuirostris*
Newell's Shearwater	*Puffinus newelli*
Audubon's Shearwater	*Puffinus lherminieri*
Fork-tailed Storm-Petrel	*Oceanodroma furcata*
Leach's Storm-Petrel	*Oceanodroma leucorhoa*
Band-rumped Storm-Petrel	*Oceanodroma castro*
Sooty Storm-Petrel	*Oceanodroma tristrami*
White-tailed Tropicbird	*Phaethon lepturus*
Red-tailed Tropicbird	*Phaethon rubricauda*
Red-footed Booby	*Sula sula*
Northern Gannet	*Sula bassana*
Pelagic Cormorant	*Phalacrocorax pelagicus*
Frigatebirds	*Fregata* spp.
Common Eider	*Somateria mollissima*
King Eider	*Somateria spectabilis*
Steller's Eider	*Polysticta stelleri*
Oldsquaw	*Clangula hyemalis*
White-winged Scoter	*Melanitta fusca*
Red-necked Phalarope	*Phalaropus lobatus*
Red Phalarope	*Phalaropus fulicaria*
Pomarine Jaeger	*Stercorarius pomarinus*
Parasitic Jaeger	*Stercorarius parasiticus*

APPENDIX 1. COMMON AND SCIENTIFIC NAMES OF INVERTEBRATES, ELASMOBRANCHS, FISHES, BIRDS, AND MAMMALS MENTIONED IN TEXT (CONTINUED).

Common name	Scientific name
BIRDS (CONTINUED)	
Long-tailed Jaeger	*Stercorarius longicaudus*
South Polar Skua	*Catharacta maccormicki*
Herring Gull	*Larus argentatus*
Western Gull	*Larus occidentalis*
Glaucous-winged Gull	*Larus glaucescens*
Glaucous Gull	*Larus hyperboreus*
Black-legged Kittiwake	*Rissa tridactyla*
Sooty Tern	*Sterna fuscata*
Brown Noddy	*Anous stolidus*
Dovekie	*Alle alle*
Common Murre	*Uria aalge*
Thick-billed Murre	*Uria lomvia*
Pigeon Guillemot	*Cepphus columba*
Ancient Murrelet	*Synthliboramphus antiquus*
Parakeet Auklet	*Cyclorrhynchus psittacula*
Least Auklet	*Aethia pusilla*
Whiskered Auklet	*Aethia pygmaea*
Crested Auklet	*Aethia cristatella*
Tufted Puffin	*Fratercula cirrhata*
Horned Puffin	*Fratercula corniculata*
MAMMALS	
Gray whale	*Eschrichtius robustus*

[1] Phylogenetic order follows Hart (1973).

[2] Phylogenetic order and common names follow the American Ornithologists' Union (1983, 1985, 1987, 1989), and phylogenetic order for species occurring outside of North America follows Morony *et al.* (1975).